MIGRATION: MECHANISMS AND ADAPTIVE SIGNIFICANCE

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COVER PHOTOGRAPH

A group of northern shovelers (***Anas clypeata***) flies north along Mustang Island, Texas Gulf beach shoreline, 3 May 1983. Thousands of ducks, herons and shorebirds fly north along the coast during peak spring migration periods at the end of April and early May. Several striped mullet (***Mugil cephalus***) can be seen in the surf zone, where they feed throughout much of the year.

Photograph taken with a Nikon F3 and Nikon 600 mm f5.6 lens on Ektachrome 400 at 1/2000 sec, f8. © 1984, **A.F. Amos**. Reproduced by permission.

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EDITOR'S NOTE

This monographic volume on migration is being offered by the University of Texas at Austin as part of its Centennial Celebration.

The symposium and resulting proceedings were organized and prepared under the aegis of Dr. Mary Ann Rankin and her committee, Drs. David Checkley, John Cullen, Christopher Kitting and Peter Thomas.

The ***Contributions in Marine Science*** considers these papers to be a signficiant contribution of academic value.

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PREFACE

Organization of the Symposium

This volume represents the proceedings of a symposium held 30 October to 2 November 1983 at The University of Texas Marine Science Institute at Port Aransas, Texas. The meeting was held as a part of the centennial celebration of The University of Texas. Its purpose was twofold: to celebrate the founding of the primary research university in the great state of Texas by bringing together scientists from around the world to discuss a topic of significant general interest, and to acquaint the general scientific community with the facilities of our Marine Science Institute.

Preparation of This Volume

Manuscripts included in this volume were submitted at the time of the symposium or within ca. 2 months afterwards, were reviewed by at least two outside reviewers, and were revised according to reviewers comments. Several submitted manuscripts were not accepted after review. The symposium was organized by Drs. David Checkley, John Cullen, Christopher Kitting and Peter Thomas of the Marine Science Institute and myself in collaboration with seven convenors: Drs. Martin Angel, Hugh Dingle, Sidney Gauthreaux Jr., Ivan Heaney, William Herrnkind, William Leggett, and William Z. Lidicker Jr. The convenors each issued invitations to the invited speakers for their respective sessions, oversaw the reviewing of the proceedings manuscripts, and wrote introductions to each of the chapters in this volume as well as contributing papers of their own. Neither the symposium itself nor this volume would have been possible without their help. On behalf of the Symposium Organization Committee and The University of Texas I take this opportunity to express my deep appreciation for their efforts.

Each member of the Symposium Organization Committee contributed to the editorial and review process of at least one chapter; John Cullen co-edited the chapter on phytoplankton, David Checkley the chapter on zooplankton (these two chapters have been combined as one in this volume); Christopher Kitting co-edited the chapter on benthic invertebrates and Peter Thomas, the chapter on fish. Others who have contributed substantially to the preparation of this volume include Mr. Christopher Thompson who helped to edit the avian papers, Ms. Robin Perkins who did much of the computer work, and Mr. Boyd Merworth and Mrs. Leslie Kjellstrand who assisted us in learning and using the Unix text processing system and the phototypesetter at The University of Texas. I also wish to thank the editorial staff of the journal, ***Contributions in Marine Science***, Mrs. Ruth Grundy, Mrs. Rebecca West and Dr.

Donald Wohlschlag, Editor in Chief, who were immensely helpful in the copyediti

One of the reasons the convenors and Symposium Organization Committee decided to publish this volume as a supplement to the journal, ***Contributions in Marine Science***, which is published at The University of Texas Marine Science Institute, was to draw attention to the unique and excellent opportunities for research that exist at the Institute. Thus as a part of the preface to this volume, I include a brief description of the Institute and the Aransas area.

The Marine Science Institute and Its Environment

Within easy reach of the University of Texas Marine Science Institute are diverse marine and estuarine environments of interest to scientists in many areas of research. These include the open Gulf of Mexico beyond the shelf-slope break, shallow waters of the continental shelf, bays, lagunas, wind-tidal flats and fresh-to brackish-water marshes. The institute is near both the Aransas Wildlife Refuge and the Padre Island National Seashore. The area is on the major north-south flyway for many avian migrants and the monarch butterfly and is the overwintering ground for some avian species, most notably the whooping crane.

The Institute is located about 40 miles northeast of Corpus Christi, Texas on the northern end of Mustang Island, a subtropical barrier island between Corpus Christi Bay and the western Gulf of Mexico (27°50'N and 97°03'W). The climate is classified as dry subhumid with an average annual rainfall of 72 mm (28.5 inches) compared to Port Arthur's 141 mm (55.4 inches) to the north and Port Isabel's 65 mm (25.8 inches) to the south. Greatest yearly rainfall was 122 mm (48.2 inches in 1888 and least was 14 mm (5.4 inches) in 1917. Snow is a rare event. Average annual temperature (measured at nearby Corpus Christi) is 22°C with extremes seldom reaching 38°C or falling below 0°C on the coast.

The laboratory provides easy access to the rich and varied south Texas marine environments. The open Gulf of Mexico seaward of the barrier islands and bay or estuarine environments found inland of the islands are two distinctly different marine ecosystems which investigators at Port Aransas may utilize. Wide ranges of temperature, salinity and turbidity characterize the waters of the area both seasonally and geographically; consequently these waters support a diverse assemblage of plants and animals.

The Gulf of Mexico—The ***soft bottom*** of the Gulf along the continental shelf supports a variety of organisms. Off Port Aransas the shelf is broad (average width 88.5 km) and gently sloping (2.3 m/km) with sediments grading from fine sand inshore to silt and clay along the middle and outer shelf. A short 20-min trawl in the shallow, sandy inshore areas will reveal large blue crabs (***Callinectes sapidus***), several species of shrimp (***Penaeus duorarum***, ***Trachypenaeus constrictus***, and ***Xiphopenaeus kroyeri***), sea pansies (***Renilla mulleri***) and numerous other invertebrates. Further offshore (water depth ca. 45 m) one typically finds deepsea starfish (***Tethyaster vestitus***, ***Astropecten cingulatus***), rock shrimp (***Sicyonia***

stimpsoni), frogcrabs (***Raniaoides louisianensis***) black sea bass (***Serranus atrobranchus***), batfish (***Ogocephalus*** sp.) and frogfish (***Antennariidae***).

The ***open waters*** of the Gulf of Mexico off the southern Texas coast are of three types: (1) the highly productive inshore zone dominated by input from Texas rivers, (2) an offshore zone which receives discharge from the Mississippi River and (3) a zone of transition between the other two. Inshore phytoplankton productivity and zooplankton abundance are correlated with peaks of nutrient input from rivers which occur each spring and fall. During these peak periods, plankton biomass and density are extremely high, many times greater than in offshore waters. Water temperature, salinity, and turbidity vary seasonally inshore but are relatively constant in offshore areas. Bottom waters in all three zones are usually turbid and exhibit high phytoplankton densities.

Sargassum weed and the blue-green alga, ***Trichodesmium*** are the most conspicuous plants in these waters. The Portuguese man-of-war (***Physalia physalia***), the purple storm shell, (***Janthina janthina***), and the sailor-by-the-wind (***Velella velella***) are common surface floaters. Flying fish (Exocoetidae) and the Atlantic needle fish (***Strongylura marina***) are frequently encountered, as are sailfish (***Istiophorus platypterus***), bonita (***Euthynnus alletteratus***), kingfish (***Scomberomorus cuvalla***), Gulf menhaden (***Brevoortia patronus***) rough scad (***Trachurus lathami***), and pinfish (***Lagodon rhomboides***). Inshore bottom dwellers include the bighead sea robin (***Prionotus tribulus***), the Atlantic threadfin (***Polydactylus octonemus***), and the southern kingfish (***Menticirrhus americanus***). Species which only occur offshore include the Mexican sea robin (***Prionotus paralatus***), the wenchman (***Pristoipomoides aguilonaris***) and the squid ***Loligo pealii***, which lives near the bottom during the day and feeds on the surface at night.

The Gulf ***hard bottom*** is the least common of the four Gulf habitats. It includes some natural rock reefs, offshore petroleum production platforms, and man-made rock jetties. The natural rock reefs are primarily in deep waters, 3 miles or more offshore, some occurring below the normal penetration of light. The steel legs of the petroleum platforms, on the other hand, extend from the surface of the water to the bottom and provide unique opportunities for the colonization of sessile marine plants and animals in the photic zone. Some of these develop communities characteristic of tropical reefs. Inshore "hard bottom" habitat, such as the granite rock jetties that line Aransas Pass, in contrast, is inhabited by organisms that can withstand great diversity in temperature and salinity. The jetty community below the water line is composed of tunicates, anemones, soft corals and macroalgae, while above the water line it is made up of organisms adapted for extended periods of exposure to air including numerous mollusks, barnacles and some crustaceans.

Bays and Estuaries—All Texas bays except the Laguna Madre are positive estuaries in which river discharge is sufficient to lower upstream salinities. In the Laguna Madre located off the coast of semi-arid land in extreme South Texas, the lack of rainfall or other fresh water input results in salinities which periodically rise well above salt concentrations in the adjacent Gulf of Mexico. The estuaries are rich with

diverse marine habitats including, ***Spartina*** marshes, mangrove swamps, seag' beds, oyster reefs, wind tidal flats and open bays.

Open bay waters (areas in the bay where the bottom is not covered by se beds or oyster reefs) are common in Corpus Christi, Nueces, Aransas, and (pano Bays. The temperature and salinities in these waters vary depending on the amount of stream discharge and the season. The average water depth is 2 meters but light penetration is restricted due to persistant high winds that keep muddy bottom sediments suspended and thus prevent the establishment of seagrass beds in these areas.

The nutrient-rich waters of the open bay support large numbers of diatoms (***Rhizoslenia***, ***Asterionella***, and ***Cosinodiscus***) in the winter and dinoflagellates in the summer which are prey for bay zooplankton (***Acartia tonsa***, ***Calanus***, and barnacle nauplii). The larvae of many of the commercially important shellfish and finfish feed, in turn, on the rich zooplankton fauna as do Coelenterates such as the cabbagehead jellyfish (***Stomolophus meleagris***), the moon jellyfish (***Aurelia aurita***), and the Ctenophore (***Beroe ovata***) which are abundant in the spring and summer. The squid ***Lolliguncula*** and various fish species including the mullet (***Mugil cephalus***), bay anchovy (***Anchoa mitchelli***), and the Gulf menhaden (***Brevoortia patronus***) may also be found feeding in open bay waters.

The open bay bottom sediments are mud, sand or a mud/sand mixture. The predominant invertebrate species in this habitat are burrowing polychaete worms (***Mediomastus californiensis*** and ***Streblospio benedicti***), infaunal bivalves (***Mulinnia lateralis***, ***Abra aequalis***, and ***Lyonsia hyalina***) and the hemichordate ***Balanoglossus*** sp. Three species of ***Penaeus*** shrimp frequent open bay bottoms in the spring and summer. These shrimp species along with blue crabs and bottom-dwelling fish such as the southern flounder, ***Paralichthys lethostigma***, croaker, ***Micropogonias undulatus*** and the black drum, ***Pogonias cromis*** are caught by small bay shrimp boats that work these waters in the warmer months.

In the shallower portions of the bays, where the water is usually less turbid, extensive ***seagrass beds*** occur. The largest beds are found in the Laguna Madre but smaller stands also occur in Aransas, Redfish and Corpus Christi Bays. Seagrass species found in Texas bays include turtlegrass, (***Thalassia testudium***), widgeon grass (***Ruppia maritima***), shoal grass (***Halodule wrightii***), manatee grass (***Syringodium filiforme***), and clover grass (***Halophila engelmanni***). This habitat is extremely productive. It is an important source of food for detritivores in the seagrass-based food web and provides food, shelter, and a place for attachment for many species of plants and animals. Shoalgrass is the principal food item of the redhead and pintail duck and supplements the diet of the lesser scaup in the Laguna Madre. Epiphytic micoralgae, diatoms, and serpulid polychaetes which attach to the seagrass blades, are food for small gastropod molluscs (***Bittium varium***, ***Anachis avara semiplacata***) and small penaeid shrimp which, along with juvenile red drum (***Sciaenops ocellatus***) and croaker (***Micropogonias undulatus***) use the seagrass beds for refuge from predators.

In areas where the salinity is between 10-30% and plankton are abundant, ***oyster reefs*** develop built up by countless ***Crassostrea virginica*** (American oyster) individuals, living and dead. The reefs are usually formed perpendicular to the predominant current and along its edge where current-borne food (phytoplankton) is most available. Such reefs are important as attachment points for sedentary animals such as the hook mussel (***Isachadium recurvum***) the anemone (***Aiptasiomorpha texaensis***) and the slipper shell limpet (***Crepidula fornicata***). The reefs also provide food and shelter for numerous motile vertebrate and invertebrate species regarded as oyster pests, such as the blister worm (***Polydora websteri***), the boring sponge (***Cliona celata***), the oyster paddock (***Diplyothyra smythii***), and the oyster drill (***Thais haemostoma***). Small stone crabs (***Menippe mercenaria***) seek refuge between the cracks and crevices formed by the oysters growing together while adult crabs dig burrows at the base of the reef. The skillet fish (***Gobiosox robustum***) clings to the reef with a sucker that is formed jointly from the underside of the belly, pectoral and ventral fins.

Communities of black mangrove (***Avicenna germinans***), occur in the bays and estuaries along the waters edge or other areas subject to tidal inundation. In the three major passes south of Galveston, Pass Cavallo, Aransas Pass, and Brazos Santiago Pass, these plants are found in dense enough concentrations to be called ***mangrove swamps***. The second largest of these swamps on the Texas coast covers 600 hectares on Harbor Island, a low barrier island located at the confluence of Aransas Pass, Lydia Ann Channel, Aransas Channel and Corpus Christi Channel. The swamp covers the majority of the land area and lines the numerous tidal channels that dissect the island. The margins of these channels are shared by ***Spartina***.

Mangrove swamps are typically extremely rich in species diversity. Striped mullet (***Mugil cephalus***), red drum (***Sciaenops ocellatus***), spotted sea trout (***Cynoscion nebulosus***) and the blue crab (***Callinectes sapidus***) use this habitat as a nursery area and feeding ground. Wading birds like the least bittern (***Ixobrychus exilis***), the black crowned night heron (***Nycticorax nictiorax***), and the clapper rail (***Rallus longirostris***) hunt small fish and fiddler crabs (***Uca*** sp.) among the tangled roots of the mangrove.

The major emergent aquatic vegetation along the shallow margin of South Texas bays (except the hypersaline Laguna Madre) is smooth cordgrass (***Spartina alterniflora***). This species attains its maximum growth midway between high and low tide levels and like the mangrove, is an important contributor of nutrients from upland sources to the coastal food web. Most of the animals living in the ***Spartina marsh*** habitat depend on the living plant as refuge and not as food.

The marsh periwinkle (***Littorina irrorata***) feeds on plant matter and detritus in the muddy bottom around the base of the ***Spartina***. This small snail climbs up the grass stalk to avoid the rising water at high tide and then descends to the sediment surface to feed as the tide recedes. Fiddler crabs (***Uca*** spp.) also feed on plant material and detritus exposed during the low tide and use the ***Spartina*** as a refuge from predators. The ribbed mussel (***Geukensia demissa granosissima***), which anchors itself in the sediment at the base of the ***Spartina***, and the polychaete ***Laeonereis***

cluveri are common subtidal invertebrates in this habitat. ***Sesarma*** crabs, which feed on the oldest outer leaves of the ***Spartina*** and any fiddler crabs it can catch, and a pulmonate mollusc (***Melampus bidentatus***) that feeds on diatoms and other algae as well as on ***Spartina*** and decayed animal matter are two species which actually consume the cordgrass.

Large portions of the south Texas bay shorelines are classified as ***wind tidal flats***. This broad, level habitat covers hundreds of square miles of shoreline on the leeward side of the Laguna Madre. Only during extreme high tides from storms or periods when the winds blow water onto these flats is there sufficient moisture to maintain a marine ecosystem. Most of the time the flats are dry and exposed to constant winds, high temperature, and hypersalinity, and are therefore not suitable for the establishment of typical salt marsh plants. Only the hardiest species such as the filamentous green algae, ***Lyngbya*** sp. can tolerate the extremes of temperature, salinity, and periodic flooding and dessication. This microscopic alga forms a sheetlike, homogeneous, leathery mat over the surface of the tidal flat. The mat, in turn provides food and shelter for microinvertebrates (protozoans, nematodes, and harpacticoid copepods) and a variety of salt tolerant insects such as ***Tachys pallidus*** and ***Diplochaetus lecontei***. When the flats are flooded, small fish (***Cyprinodon variegatus*** and ***Fundulus*** spp.) feed on the mat and the insects that have been trapped by the rising water. During this period shorebirds also come to the flats to feed on these small fish and insects. When the waters recede, the fish that have survived the bird predaton return to the Laguna Madre.

The Facilities

MSI includes 82 acres of ocean front land and 100,000 square feet of laboratory space, a 14,000 square foot physical plant, a four-acre boat basin, 17 apartments, 16 dormitory rooms and a mess hall. The Institute operates a variety of research vessels including the 85-ft LONGHORN, the 57-foot KATY, and a half dozen smaller boats for bay work. The laboratory includes both a scientific staff and a physical plant support staff; facilities are available for visiting scientists and students year-round. Inquiries regarding short- or long-term accommodations should be addressed to: Dr. Robert Jones, Director; The University of Texas Marine Science Institute; Port Aransas, Texas 78373, U.S.A.

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INTRODUCTION

The amazing feats of orientation, homing, and distance that some migrants display have awed human observers for centuries and still present exciting challenges in research. Migration is a major factor in the life history of countless organisms and draws the interest of ecologists, physiologists, geneticists, behaviorists, evolutionary biologists, and theoreticians. This symposium and its proceedings volume were organized in the spirit of this general interest. The papers in this volume are grouped along taxonomic lines and reflect the organization of the symposium. Contributions include both general reviews and research reports. In addressing the topic of migration widely and in the context of a symposium, we have not been able to cover all aspects of research in migration/dispersal in each group, but we have presented a variety of approaches and summaries of results that we feel represents current thought in the area and suggests fruitful areas for future research. Readers are encouraged to forage across chapters for work that addresses similar questions in different groups and to discern general principles, parallels, or differences for themselves.

In spite of, or perhaps because of the enduring and widespread interest that migration has elicited, there exists a history of disagreement concerning what it actually is. To the person studying movements of birds or mammals, migration usually means long-distance "round-trip" movement from a summer or wet-season range to a winter or dry-season range, while movement that takes the organism permanently away from its natal area is dispersal. Many horizontal aquatic migrations involve a return of individuals to the area of origin, but others are reminiscent of common insect movement patterns and involve passive transport on ocean currents to breeding or feeding areas with return to the point of origin being performed by a subsequent generation. To scientists studying plankton, migration is movement (usually vertical and diel) between areas rich in nutrient to areas that support photosynthesis, or movement to and from areas of high prey density but high predation risk. Although at first glance vertical migration of plankton may seem a different phenomenon from horizontal movements of other organisms, in terms of frequency during the life cycle and function served, such movements are not unlike the round-trip migrations of vertebrates. Entomologists have come to consider many types of movement migration, and it is unusual if return by the same individual to the departure area occurs. A further complicating factor in defining or even discussing migration is, as Taylor and Taylor (1983) point out, that migration in an ecological or genetic context may include quite different types of movement than would migratory behavior.

Disagreements in definition are more than semantic argument; they reflect basic differences in approach and in the kinds of questions being addressed. They may even contribute to erroneous assumptions such as the long-held belief that because many insect migrants do not precisely direct their flight path and do not, as individuals at least, return to the natal habitat or point of origin, migration in such cases must be nearly the equivalent of genetic death, favored only under the most adverse conditions

or, in group selection arguments, because of benefit to the resident, nonmigrant population. What types of movement should be considered migration, and how they may relate to one another are complex questions that form a subtle barrier to synthesis and generalization across systems. With his characteristic clarity and brilliance, John Kennedy in the first paper of this volume, attacks the definition barrier once again and sets the stage for the diverse papers in the 6 chapters that follow. He also discusses the general principles and questions that can be discerned in the wide array of movement patterns called migration and/or dispersal.

In the second paper of the volume, Hugh Dingle discusses the broad question of the role of migration in life history. Once again generalizations depend somewhat on one's definition of migration, but Dingle suggests some general principles and areas for future research. One question that emerges from Dingle's discussion and from many other papers in this volume is that of the "cost" of migration or dispersal. Some knowledge of the cost or benefit of migration is essential to understanding either its role in the life history of a species or its evolution. The long-held view that migrants incur great cost in terms of risk of death or injury en route, energetic demands of the trek, and/or delayed or diminished reproduction is being addressed in many groups both experimentally and theoretically. Papers by Denno, Palmer, Zera and Solbreck in this volume each address this question in insect systems. Zera documents actual fitness differences between winged and wingless waterstriders. The other three authors, in contrast, suggest that under some circumstances the cost of migration in insects may be less than previously supposed, particularly when the costs of staying are weighed against benefits in a new habitat; long-distance movement may form part of a colonizing life history strategy in which migration and reproductive output are both maximized. Leggett discusses the role of migration in the life history evolution of fish, suggesting that migration can and does greatly reduce the impact of environmental variance on reproductive success. Dodson, Lambert and Bernatchez assess the energetic costs of migration and reproduction in two species of anadromous coregonines. These authors find that energetic costs of migration are high in both, but neither species behaves so as to minimize that cost. Again in fish, Miller, Crowder and Moser analyze the cost/benefit ratio of migration to estuarine nursery areas. Alerstam discusses the energetic costs and benefits associated with different flight patterns in arctic and common tern migrations and shows that energy use during these amazing flights from northern tundra to Antarctic pack ice accounts for nearly one quarter of the total energy budget of the species.

A related question addressed in several chapters concerns the use of passive transport mechanisms by migrants to reduce the energetic cost of long-distance movement. For example, when fish such as plaice, sole, cod, and eel move up off the bottom and into moving tidewater according to the direction and speed of the water movement, they are exploiting the tide for passive transport and reducing the costs of movement. Similarly many fish travel long distances in ocean currents and reduce both energy and time required for long-distance travel. The currents may also provide an orientation cue on long swims. (See McCleave, Arnold, Dodson and Neill 1984 for several reviews.) These behaviors resemble the flight strategy of many insect

migrants that after take-off, fly up past their boundary layer and are carried long distances by prevailing winds. The insects are thought to determine the direction of travel by controlling altitude and time aloft and by choosing, in response to appropriate environmental cues, the appropriate day and time of day to go aloft. In this volume, McCleave and Kleckner model the passive drift of eels in ocean currents, and Heyerdahl, in a beautiful summary of his life's work, documents the movements of early civilized man across the major oceans by passive drift. Richardson discusses use of the wind and weather fronts by birds in flight, while Schmidt-Koenig, Walker, Solbreck, and Brower each address this question in insects.

Orientation mechanisms also show common trends as well as differences across systems. Certainly for passive migrants, orientation within the transporting medium to exploit but not be at the mercy of the medium is a general need; but data on the extent to which passive migrants actually accomplish this ideal and the mechanisms by which they may do so are difficult to obtain, since such studies usually require following the migrants en route. Radar studies on African locusts and other insects have provided the best information for insects (see Rankin and Singer 1984; Rainey 1978 for reviews). In this volume, Schmidt-Koenig and Walker each discuss orientation to wind by butterflies and Solbreck analyzes long-range movement and settling in a lygaeid bug and the spruce bark beetle. Richardson and Alerstam both discuss orientation of birds to prevailing winds. McCleave and Kleckner address orientation in the transport medium by eels; Hamilton describes similar behavior in molluscs. Heyerdahl gives an elegant explanation of ocean navigation by early man.

Orientation to cues other than the transport medium has been studied in many different systems. Able and Cherry summarize and evaluate recent work on orientation and navigation in birds, and Bingman, Beck and Wiltschko analyze the ontogeny of migratory orientation in the pied flycatcher ***Ficedula hypoleuca***, particularly implicating the earth's magnetic field as a primary source of orientational information. Baker argues that humans and other mammals can also orient via the earth's magnetic field, while Schmidt-Koenig and Brower each discuss this possibility and other orientation mechanisms for the monarch butterfly. Walker analyzes orientation of several fall-migrating butterflies in the southeastern U.S., Herrnkind reviews his work on orientation mechanisms in migrating lobster, and Hamilton describes some fascinating experiments on orientation of migrating ***Aplysia***.

The adaptive significance and evolution of migration are discussed by many authors in this volume, however, Gauthreaux, and Ketterson and Nolan analyze these questions in avian systems, and Quinn addresses the evolution of homing and straying in sockeye salmon. Brandt, in an empirical study and Kiester, using a theoretical model discuss various aspects of sex-specific dispersal in small vertebrates.

The cues that induce and terminate migration have interested scientists as well as casual observers. Photoperiod, temperature, food quality or quantity, and other aspects of habitat quality have all been shown to elicit movement or settling in some systems. This general topic is addressed in different ways by many of the contributors. Angel, Kerfoot and Huntley all discuss the factors that induce migration of zooplankton; Heaney, Sommer, Klemer, and Kamykowski each analyze reasons for

phytoplankton movements, with Kamykowski contributing some specific methodological suggestions for research in this technically difficult area. The paper by Kitting on the diel migration of a small mollusc in a seagrass community provides an interesting echo to those on plankton. Wolcott and Wolcott assess the possible causes for migration of terrestrial and intertidal crustaceans, Scheibling does the same for sea star movement, and Herrnkind analyzes proximal causes of lobster movement. Fenton and Thomas review what is known of factors involved in bat movements, while McCullough gives an excellent general summary of long-range movement of large terrestrial vertebrates. Gauthreaux, and Ketterson and Nolan discuss reasons for migrating or not migrating and cues involved in settling for birds.

Investigations of physiological changes that induce migration or dispersal have revealed some interesting parallels between small mammal dispersal and insect migration. Tendency for movement away from the natal habitat in both is frequently associated with the prereproductive period, and the suggestion that hormones involved in reproductive development may also influence migratory movements has been made in both systems (see Holekamp, Simpson and Smale; Rankin; Herman; Brower, this volume). Herrnkind briefly considers the question of probable physiological controls of lobster migration, and Berthold summarizes physiological changes associated with migration in birds.

The genetics of migratory behavior or migrant morphology is an extremely important area that has not been addressed in many systems. In this volume, Zera and Palmer in insects and Berthold in birds discuss their results in this critical area.

Mary Ann Rankin

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MIGRATION, BEHAVIORAL AND ECOLOGICAL

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ABSTRACT

Movements called migrations vary so much in mode and scale among animals that it has proved difficult to arrive at agreed generalizations. There is now no consensus even among students of insect migration. Two different ways of escape from the prevailing confusion of concepts and terminology have recently been proposed. R.R. Baker argues that migratory behavior should be regarded as an aspect of exploratory behavior: a view here judged untenable. On the other hand L.R. and R.A.J. Taylor argue convincingly that migration as an *ecological* process must be defined at the ecological level: it is population re-distribution by movement, whether or not the movement is controlled by the animal through some specialized migratory behavior. A general definition of specialized migratory ***behavior*** is offered with illustrations showing that it cannot be regarded simply as extended foraging behavior. Previous definitions of migration have tried to combine ecological and behavioral criteria but failed because by no means all population-redistributing movements involve any specialized migratory behavior. Some major evolutionary factors that may explain the great diversity of migratory behaviors are briefly surveyed. Clear recognition of the distinction between the ecological and behavioral meanings of migration is enough to remove the current confusion and offers hope of eventual objective criteria for other, complementary concepts such as "habitat," "trivial movement" and "station-keeping." Quantitative comparison of track patterns inside and outside areas deemed to be units of habitat is necessary for this but has hardly begun.

INTRODUCTION: BEHAVIORAL SPECIALIZATION

Integrating the subject of migration among animals generally is not easy because perceptions of what migration is depend so much on the particular animals elected for study: their size, mode and medium of locomotion, life strategy and so on. This contribution is colored by experience of insect migration, but there is an exceptionally rich store of information on insect migration as has often been said (e.g., by Taylor and Taylor 1983, p. 187). Not the least of the insects' merits in the search for general principles is that they span the critical range of sizes from birds and mammals down to the microscopic. This variety enabled students of insect migration to make progress in the last two decades towards a consensus on what migration is, at least in behavioral terms, and many of us believed this was comprehensive enough to cover other animals

too (e.g., Southwood 1981). The recognition that even the so-called dispersals of small, feeble insects are not typically accidental but adaptive (Johnson, 1969) meant that "migration" could now embrace them as well as the self-propelled traveling of larger animals, from insects to whales, for which the term was once reserved; while special terms such as ***emigration*** and ***nomadism*** could be reduced to sub-categories of the overall phenomenon, migration.

As an insect ecologist reviewing the ecology and evolution of migration in animals generally, Dingle (1980) carried the trend to its logical conclusion by stripping away all particularities to arrive at this general definition:

> Migration is specialized behavior especially evolved for the displacement of the individual in space.

Dingle had started out from a particularized behavioral definition of insect migration (below) but then jettisoned it, presumably because there are many obvious exceptions to it outside the insects. Unfortunately, paring down the concept of migration to the point of complete universality in this way, although logical, leaves the definition with little substance. The resulting definition centers on behavioral specialization but can specify no more than its common outcome, spatial displacement; there is no common type of behavior that can be identified as causing migratory rather than nonmigratory spatial displacement.

A definition without exceptions is hard to find in biology and as in this case can be achieved only at the cost of content. With that is lost its usefulness as a starting point for recognition and analysis of specific cases, thus defeating the object. If a more explicit definition is generally, although not universally, applicable, then not only does it provide such a starting point but each exception to it becomes a "natural experiment," raising answerable questions about the special conditions that make it an exception and thus about the conditions for the general case too. If this reasoning (cf. Southwood 1977) is valid, we need a more particularized behavioral definition and can go back to the one from which Dingle (1980) started. It referred to insects but may also be applicable, with some exceptions and some amendment, to animals generally:

> Migration is persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it. It may be effected by the insect's own locomotory exertions or by its embarkation on some transporting vehicle, and in common with diapause involves a phase of depression of "vegetative" (growth-promoting) functions as a condition for their resumption (Kennedy 1961).

On reflection, it will be apparent that each of those particular characteristics is comprehended under the single word ***travel*** as we apply it to our own behavior in ordinary speech. This word is used again and again without a second thought throughout the migration literature, which gives one some confidence in the general usefulness of the definition, unwieldy though it be. It does not attempt to define a watertight category with every case displaying the specified characteristics in equal degree. Rather, it attempts to define the common ***direction*** of specialization evident

in the behavior of migrants (also Kennedy 1975, Kennedy and Way 1979).

Behaviorally, "vegetative functions" are activities that exploit the available resources for growth: somatic growth in juveniles and adults and growth of the genital and accessory products in adult sexual maturation. They include a variety of localizing, station-keeping behaviors in association with foraging (followed by feeding) and with reproductive behaviors following sexual maturation: mate-finding, mating, oviposition-site finding, nesting, oviposition or parturition, parental care, etc. Some inhibition of these responses seems to be a constant feature of migratory behavior; whereas the behavior by which the movement itself is executed is highly variable. "Vegetative stimuli" include those betokening not only food but also the associated resources required for the effective vegetative existence of the species: stimuli from shelter, resting sites, mates and other conspecifics, mating sites, nest sites, landmarks, microclimate, etc.

Note that the definition gives "some" internal inhibition of vegetative activities as a criterion of migratory behavior. Baker (1978, p. 18; likewise Taylor and Taylor 1983) dismissed that key criterion on the grounds that the inhibition of vegetative responses is neither total nor maintained for twenty-four hours a day, which suggests he must have overlooked the word "some." Feeding does of course sometimes interrupt migratory locomotion which demands fuel for the muscles. This feeding may provide material for growth as well, but that is while reproductive behaviors are inhibited, before sexual maturity, so there is again some inhibition of vegetative activity. Mating and oviposition also sometimes interrupt migratory locomotion, or occur at other times in the same day, like roosting—to mention three further types of vegetative activity mentioned by Baker. Segregation of migratory and vegetative activities into separate periods of the day (quantified, for example, by Caldwell and Rankin 1974) illustrates rather than contradicts the inhibition of vegetative activities during migratory behavior.

On the other hand Baker (1978, p. 5) brought out a serious defect in my 1961 definition of migratory behavior quoted above. Like Johnson's (1969) definition of migration, it covered only movements from one vegetative habitat site to another. It omitted movements to and from non-vegetative sites where no breeding occurs: sites of diapause, dormancy, hibernation, aestivation, etc., hereafter referred to collectively as "diapause sites." The wording of the 1961 definition implied that the responses that are more or less inhibited when the movement starts are the same as those that eventually arrest it, but this cannot be generally true of movements to and from diapause sites. Thus migration from a vegetative to a diapause site begins with some inhibition of the station-keeping responses to vegetative stimuli but it is eventually arrested, not by them, but by station-keeping responses to different, non-vegetative stimuli from the diapause site (e.g., Landin and Vepsäläinen 1977).

However, repairing that omission does not affect an important point in the 1961 definition, namely, that the migratory activity is a condition for the development of responsiveness to the stimuli that eventually arrest it (e.g., Foster 1978; other examples in Kennedy 1966 et ante, 1975). This is probably true of migrations to and from diapause sites as well as those between two vegetative sites. A classic

illustration from applied entomology concerns coccinellid beetles that hibernate in the mountains and in the spring fly down to lowland orchards, their vegetative habitat. When beetles ready to migrate were collected from their mountain hibernacula, carried down to the orchards and released there, they refused to behave as the operators hoped. Instead of staying to prey on the aphids there, they flew away—in the same direction as they normally would have taken from the mountains (Williams 1958, p. 94).

An amended definition would then be:

> **Migratory behavior is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation on a vehicle. It depends on some temporary inhibition of station-keeping responses, but promotes their eventual disinhibition and recurrence.**

INTEGRATIVE LEVELS

Meanwhile there have been two proposals for radical re-integration of the whole subject, one at the ecological level by Taylor and Taylor (1977, 1983), and one at the behavioral level by Baker (1978, 1981, 1982). Both parties maintain that migration studies have become too parochial, losing touch with the natural context and altogether too preoccupied with diverse behavioral mechanisms supposedly peculiar to migration but defying generalization. Both parties define migration in such a way as to include movements over any distance no matter how small:

> A change of place between generations (Taylor and Taylor 1983);
>
> The act of moving from one spatial unit to another (Baker 1978).

For the Taylors, migration is in the first place not an act at all but "a purely spatial concept" (1983, p. 197), not behavioral but ecological, a matter of population redistribution by movement of any kind whatsoever. It is simply

> the component of movement peculiar to population dynamics, whether controlled or not (1983, p. 184).

Movements to and from diapause sites within one generation also affect population dynamics, but they are omitted if migration is a "change of place between generations" only. This omission does not seem to be an oversight since the authors repeat it ("Survival is by movement within the population and, if it separates the birthplace of generations, we call it migration" (1983, p. 199)), and Johnson (1969) had already described migration similarly as a change of breeding place. Baker (1978, p. 5) pointed out that this description excluded, inter alia, some of the most spectacular migrations of mammals and birds, which are to and from ***non***-breeding places. Rather than repair the omission Baker took it as support for a major theme of his monumental book, that there is nothing definable about migration to justify distinguishing it from movement in general. This echoes Elton's (1927) view of

migration and it helps to explain Baker's very unspecific definition above.

The Taylors are accustomed to studying actual populations on maps (e.g., Taylor and Taylor 1979) in accordance with their sound principle of looking at the whole population when considering population dynamics, and elsewhere in the 1983 article (p. 197) they describe migration as

> the persisting change that is left over when all other, minor excursions are removed, whatever their cause or function.

So it appears that in practice they do not treat minor movements as migrations, and at first sight this amended version would be more generally acceptable. But the definition has now lost its rigor: the criterion of "minor" is subjective, for it depends on the scale of one's map. Moreover it is of course impossible to ascertain solely from a series of maps the extent to which a redistribution is in fact due to movement, as distinct from natality and mortality.

Nevertheless the Taylors' main thesis is valid. Migration is an ecological process and "an ecological property can only be defined ecologically" (1983, p. 200). Their corollary that "migration can be ***characterized*** behaviorally, physiologically, or genetically for individuals or species, but not ***defined*** at lower levels of organization" may be less convincing, but their main point that these different levels must be distinguished is compelling and new. Rogers (1983) is confident that the Taylors' approach can lead on to major advances at the ecological level since it stems from their previous achievement in breaking with the tradition of considering only time in population dynamics, neglecting space. It is now generally acknowledged that a real population "forms a continuum in space and time": the famous fern stele model of Taylor and Taylor (1977).

Their new theory of migratory ***behavior*** (the Delta Model of Taylor 1961; Taylor and Taylor 1977, 1978, 1979, 1983) is another matter. It states in effect that the movements involved in population re-distributions result from density-dependent, alternating, mutual attraction and repulsion between conspecifics (1983, pp. 202 and 207). While there is no doubt that those intraspecific locomotory reactions are real and important, the theory that they explain L.R. Taylor's ecological Power Law relating population density and spatial variance, confounds the behavioral and ecological levels. For in attributing redistributive movements in general to those particular locomotory reactions, the theory contradicts the Taylors' own point (below) that many of these movements involve no special behavior. Also, the Power Law holds for plants (Taylor, Woiwod and Perry 1978) which do not locomote. Some other objections and alternatives to the Delta Model are summarized by Dye (1983).

There is indeed widespread confusion in the literature between the ecological and behavioral levels. It is epitomized by the continual bracketing together of migration and dispersal as if these were complementary categories on the same level, or even synonyms. Southwood (1981) set out the objective relationship between these two different processes in a lucid diagram showing that dispersal, being an increase in the mean distance between individuals, is something that only a population can do; whereas migration, being movement beyond the habitat, is something an

individual also can do, a behavioral process. But the reason why people so often speak of "dispersal" instead of migration seems to be historical: they are anxious to avoid any of the old, restricted, behavioral connotations of the word migration, such as self-propulsion, unidirectionality, or regular returns, where these do not apply or are not known to apply. It is to be hoped that with the recent broadening of the behavioral meaning of migration this anxiety will be allayed and the term dispersal dropped. It is redundant at the behavioral level, and it leads again and again to the absurdity of an individual being described as dispersing, as Baker (1978) justly says. One cannot help wondering how this heroic, dismembered individual still manages to arrive in one piece.

The Taylors give a more compelling reason for keeping clear the distinction between the ecological and behavioral levels of migration:

> The definition of migration in ecology...has no equivalent in behavior or physiology (1983, p. 200).

They point out (p. 197) that at the ecological level it is impossible to draw any line between displacements during accidental or trivial movements and displacements that are "controlled," i.e., due to some special migratory behavior. Although the former are excluded from the behavioral definition of migration they must be included under the ecological definition of it: re-distribution by movement "whether controlled or not." Ecologically, migration "does not exclude 'accidental' migrants such as a foraging bee that is blown off course and unable to recover" (1983, p. 197), although this is patently not migratory behavior. A vivid example of migration by trivial movements that is quoted by both Southwood (1981) and the Taylors (1983) is the rapid and repeated re-colonization of islands that have been de-populated by flooding, which has been observed in a behaviorally nonmigrant species of beetle. Ecologically, this is undeniably migration. Moreover, no general limit can be set on the time-span of a migration in the ecological sense (Elton 1958), whereas in the behavioral sense each migration is completed in less than one life-span. Thus migration at the behavioral level is not co-extensive with migration at the ecological level; it covers a smaller class of movements.

EXTENDED FORAGING?

Baker (1978, 1981, 1982), by contrast, focuses on migratory behavior. The context into which he wishes us to re-integrate it is ***exploratory*** behavior. Exploratory behavior consists of movements during which the animal acquires and stores topographical information about the resources in its environment, and it may not stop to exploit any of them at the time, returning later for this. The proposition that long-range migrants that are found colonizing a fresh habitat area have done the trip beforehand on a non-colonizing, exploratory visit seems far-fetched. It seems incredible, too, that natural selection could allow such a laborious performance to persist when less costly options are open. Baker (1982, pp. 163–194) recognizes two groups of exceptions to the rule of prior exploration, all among invertebrates, and

explains that the first group "base their way of life" on "a sense of direction" instead of the "sense of location" achieved by exploring, while the second group are "automatons" with no sense of either. The first group includes well-known butterfly migrants and the locusts, and the second, well-known aphids and the phoretic mites (see Binns 1982). Perhaps it is not pure coincidence that these supposedly exceptional arthropods are also those whose migratory behavior is better documented than usual.

For all the other migrants, Baker stands by the exploratory theory of migratory behavior. There is no good evidence for it in long-range migrants, and as Baker says, the evidence would be very hard to obtain, whereas there is experimental evidence against it. For example, birds that have never been outside the laboratory show the seasonally "right" compass orientation on first seeing the natural starry sky (see Schmidt-Koenig 1979), and birds can be induced, by prior exposure to the appropriate seasonal daylengths, to orient their movements in opposite directions under a planetarium "sky" in conformity with the seasonally opposite directions of their migrations (Emlen 1969). The best documented case of migration among the insects and probably among all animals is that of the desert locust. This enabled Draper (1980) to check Baker's (1978) interpretations of their movements one by one: they were not borne out.

If one wishes to integrate migratory behavior into a wider behavioral context, then that surely would be ***foraging*** behavior—provided one is permitted to stretch that term to cover the locomotory maneuvers used in finding not only food but any kind of resource item: mate, oviposition site, resting place, refuge, display site, nest site, warmth and so on. For lack of a better term "foraging behavior" will be used here inclusively for all those behaviors, as Prokopy and Roitberg (1984) have recently used it. Likewise foraging for food items and searching for oviposition sites (hosts of parasitoids) are so similar that they are already often treated together (Hassell 1978).

Admittedly the term' that has long been used for behaviors of that kind is ***searching***. But this term, also, would need re-defining to make it more apt than foraging, and it is too entrenched for that now. Searching can be done with a vertebrate eye or arthropod antenna or any other independently movable receptor organ, by itself, scanning the environment without any locomotion by the animal, whereas foraging clearly means locomotion. Locomotion is the common feature that can be observed in all behaviors of this kind (de Ruiter 1967) and needs to be conveyed by their name, above all in any study of spatial displacement. "Searching" certainly implies some form of scanning (ibid.) but fails to specify locomotion. For what searching really describes is not observed behavior but a human, subjective, cerebral activity that is not observable in animals.

Foraging as therefore used here, in the context of spatial displacement, may be defined objectively as:

Reiterative locomotory activity that is readily interrupted by an encounter with a resource item of one particular kind.

That is to say, the animal's threshold of response to stimuli from one kind of resource item is particularly low at that particular time, so that when these specific stimuli are received, they readily inhibit the locomotion, replacing it by some other behavior, say eating. If the encountered resource item then disappears for some reason, such as being eaten by the animal or preempted by a rival, the locomotion is normally resumed. But if now another similar resource item is not encountered within a certain time, for the given animal, the foraging movement is again replaced by some different behavior, say resting, or emigration (e.g., Roitberg, van Lenteren, van Alphen, Galis and Prokopy 1982). If the intervals between the encounters remain shorter than that, the activity may be called "local foraging," typical of behavior within the habitat; if longer, it will be called "extended foraging" as defined strictly below.

Foraging behavior, in the inclusive sense defined above, appears to be what the Taylors have in mind as migratory behavior, for they describe desert locust migration as "basically a prolonged oviposition flight, terminated by environmental cues that anticipate improved prospects for survival of the offspring" (1983, p. 199). But the behavior of swarming desert locusts is not like that (e.g., Popov 1958, Kennedy 1951). When they reach sexual maturation their migratory flying is indeed somewhat reduced, but it is not terminated by the moist soil that is the cue for oviposition, or even by oviposition in it. They fly on, often within the day, laying eggs in widely separated places, and the places where they settle when ready to lay are not related to the suitability of the soil for laying. While they are still sexually immature, they fly more persistently and their mating and oviposition responses are totally inhibited.

If there were no phase of inhibition of responses to vegetative stimuli with their arresting, detaining effect, animals would not be able to leave a habitat until it ceased to supply enough of these stimuli. It is this inhibition of vegetative responses that underlies the impression of "undistractededness" (Johnson 1969) that migrating animals often give to an observer. If animals could never emigrate in anticipation of deterioration of the habitat, which is signaled by the decrease of vegetative sensory inputs, then behavioral migration would always be facultative, in other words always due to "current adversity," which it certainly is not (e.g., Southwood 1962).

Migration cannot be called simply extended foraging, although there is a continuous spectrum here. The sequential changes of responsiveness to conflicting environmental stimuli seen in migratory behavior, are also observable, although more frequent, during trivial foraging movements within the habitat. The female small cabbage white butterfly, for example, interrupts (inhibits) her egg-laying response to a host plant after laying only one egg on it and takes off on a brief flight. After that she becomes responsive to host plants again and therefore orients her flight to a neighboring plant, lands and lays another egg on it. The duration of the bouts of inhibition of those three vegetative responses to host plants governs the spacing out of the eggs through the habitat and is somewhat more extended in the Australian than in the Canadian habitats of the species (Jones 1977). Migratory behavior would involve

still further extension of the inhibition.

Temporary inhibition of the response to one kind of orienting stimulus in favor of another occurs repeatedly when animals are not migrating and becomes prolonged when they are. Taking desert locusts as a well-known example again, the nonmigratory, non-gregarious nymphs are attracted to vertical silhouettes and thus to the plant clumps of their desert habitat sites. This response is inhibited for periods of minutes while they leave the plants and bask in the sun on adjacent patches of bare ground. When they turn into the migratory, gregarious form, the attraction to plants is inhibited for hours every day (reappearing whenever the day becomes excessively hot). The consequent tendency to avoid obstacles facilitates their sustained traveling. The orienting stimuli to which they become most responsive on the march are the sun (as a compass) and the sight of their moving fellows in the crowd, both of which have some stabilizing effect on their direction of march (Ellis and Ashall 1957; Kennedy 1939, 1945).

It is of course the long-range orientation mechanisms that have always been the most striking and most studied component of behavioral specialization in migrants. The common characteristic here is that directional cues emanating directly from resources cease to play the dominant role in the animal's orientation behavior, a role taken over by directional cues from ubiquitous environmental features like the sun, the stars, the geomagnetic field or the wind. Being ubiquitous, these alone can provide a traveler with continuous guidance. Steering by them may serve only to stabilize the ground track, thus tending to straighten it out. This increases the animal's net displacement in space and hence its coverage of new ground. With further behavioral sophistication, migrants use those ubiquitous cues as signposts with the aid of their internal "maps," in navigating towards distant resources, as much elegant recent work has shown (this volume).

The light from the sky likewise does not come from any resource but functions as a vertical "signpost." It is no doubt involved in local foraging when that includes brief flights between landings as in the small cabbage white butterfly, and it takes over as the dominating orientation cue for numerous insect migrants that use it phototactically in embarking on their transporting vehicle, the upper wind which then straightens and stretches out their movement horizontally (Johnson 1969; Riley, Reynolds and Farmery 1983). When the insect has entered the migratory state, this climbing response to the sky light may be triggered by particular weather stimuli received on the ground, which helps to ensure that the wind vehicle will be going the "right" way at the time of embarkation (e.g., Brown, Betts and Rainey 1969; Schaefer 1976; Riordan 1979). Analogous mechanisms have been described in birds (Keeton 1981), fishes (Arnold 1981, Harden Jones 1981) and marine larvae (see Baker 1978; Angel, this volume).

Thus migratory behavior embodies in exaggerated form the basic pattern of behavioral sequencing that already operates during local foraging. Nevertheless these examples show that migratory behavior is more than extended foraging. That is to say, it is more than a simple extension, when resources are spaced further apart, of the unchanged temporal pattern of local foraging behavior. Because ***dis***inhibition of

vegetative responses sets in quickly during each bout of locomotion in local foraging, the animal is ready to respond to a new vegetative stimulus very soon. If such a stimulus is received equally soon, then the animal is arrested again within a short distance, thus tending to stay within a habitat locality where such stimuli abound. Migratory behavior is different: disinhibition of the vegetative responses during locomotion is slow, and their prolonged inhibition prevents the animal from being promptly re-arrested by another vegetative stimulus, so it keeps going.

With "obligatory" migration where the prolonged inhibition of the station-keeping responses arises from genetic causes, it is obvious that the migration is not extended foraging. This is not so obvious with "facultative" migration since the latter is due to the "current adversity" of habitat deterioration, over-crowding included. The deterioration will mean that arresting stimuli from local resources are weakening and coming in less often, or being nullified by opposing stimuli. Nevertheless, the emigration could be equated with extended foraging only if these sensory inputs, increasingly antagonistic to vegetative responses, had no cumulative effect on the animal's responsiveness to vegetative as against locomotory stimuli. That is hardly conceivable. Locomotory excitability will increase together with inhibition of the station-keeping responses, as demonstrated in the field (e.g., Turnbull 1964, Smith 1974, Waddington and Heinrich 1981, Roitberg et al. 1982) and in laboratory experiments (e.g., Thomas 1974, Traynier 1979, Chapman 1982, Kennedy 1966 et ante, Kennedy and Ludlow 1974).

Migratory behavior has differentiated and diversified so much through the animal kingdom and even within the insects that the Taylors described it as "a multiplicity of specific mechanisms" (1983, p. 201), implying that the mechanisms have little in common. But there does appear to be a recognizably common direction of specialization, and it is this that provides the much-needed starting point and frame of reference for the behavioral analysis of each particular case. Given these, it is possible to set about identifying which responses to which stimuli are relatively inhibited and which are enhanced to the point of dominating the animal's behavior for the time being.

This has yet to be done for most cases of ecologically known movements. We lack the information needed to assess whether the movement does involve special migratory behavior. The problem is acute with what is called "nomadism," where the resource itself moves—like the prey of wolves and seals, or the plankton food of fishes, or the vegetation produced by shifting local rainfall in the desert or savannah for many ungulates, birds and insects. The locomotory activity of an animal that is exploiting such a mobile resource can be notably persistent (although discontinuous), but it may look as if this is simply because it is pursuing the resource: not migrating but engaged in shifting foraging. To the extent that the pursuing animals manage to keep in contact with such a mobile resource, one might not expect to find any prolonged inhibition of the animal's responses to it or any special use of long-range "signpost" stimuli.

An instance where both of these characteristics of special migratory behavior are in fact present concerns wolves tracking their mobile caribou prey in northern Canada (see Sinclair 1983). There comes a time in the spring when the wolves cease preying on the caribou herd, although it is still at their mercy, and run ahead of it to raise families where the caribou will arrive later to raise their own families. In this way the wolves gain a richer resource in the shape of easily caught caribou young. (Somebody could have warned Little Red Riding Hood about wolves!). There are many more cases where special migratory behavior is involved in the pursuit of mobile resources, and still more are likely to be discovered if sought.

EVOLUTIONARY FACTORS

A number of factors have been identified which, it is inferred, have influenced what particular kind of behavioral specialization has occurred during the evolution of migrants. They explain why students of the migratory behavior of different animal groups have perceived and defined migration in such different ways. A major factor is the animal's power. The effects of this factor have been encapsulated in another lucid diagram of Southwood's (1981). The less locomotive power the animal has relative to that of its medium—air or water—the more the animal must rely on the movement of that medium for its traveling. Vice versa, the greater the animal's power, the more the animal can rely on its own controlled locomotion and orientation reactions and make sophisticated use of long-range "signpost" stimuli. Animals of intermediate power (large insects, small-to-medium fishes and birds) tend to combine the two techniques of directional travel, heading as well as drifting downstream thus adding their own appreciable speed to that of the current, like downstream canoeists in Southwood's (1978) analogy.

Power goes, in general, with size, making it easy to understand why small animals of insect size or less rely so much on currents of air or water. But another factor also favors this: for any given shape, the smaller the animal the more buoyant it is and the less energy it need expend on simply keeping itself aloft in the current. Energy expenditure on that is also saved by some migrant birds and insects that have acquired the arts of gliding and soaring (Alerstam 1981); these activities of course occur also in nonmigratory, foraging behavior, notably in birds of prey.

Another factor for animals big and strong enough not to rely entirely on a transporting vehicle for migration, is their locomotory mode. Swimming is energetically the cheapest mode of travel, and out of water, flying is cheaper than running (Schmidt-Nielsen 1972). The insects were the first to invent flight and not surprisingly use it for migration in the great majority of cases (Johnson 1969), shifting into a specialized, steady, cruising mode of flight when migrating (e.g., Ward and Baker 1982).

Unlike the situation in vertebrates, flight is confined to the adult stage in insects as a whole, whether they be migrants or not, and this stage (unless flightless) is also behaviorally the most sophisticated one in the life-history, being equipped with the most elaborated receptors, CNS and effectors. That kind of morphological and

physiological specialization serves the adult's exacting behavioral tasks of mating and oviposition, i.e., the correct *placing* (not growth) of the genital products. It was therefore dubbed "sensorimotor" specialization in contradistinction to the "vegetative" specialization of insect juveniles ("adults find growth resources, while juveniles exploit them": Kennedy 1956, p. 362; 1961). The adult insect is preadapted for further specialization into migratory behavior, which is also exacting, and was therefore described as "super-adult" by analogy with the "super-adults" produced by endocrine manipulation (ibid.). Presumably that is why it is at the adult stage that migratory behavior has differentiated in the great majority of insects.

Surprisingly at first sight, the minority of insects with flightless adult females have gone to the opposite extreme, differentiating migratory behavior at the earliest, smallest stage rather than any intermediate one: mealy-bugs, for example, and gypsy and winter moths whose first-instar larvae let themselves go on long silken threads somewhat like gossamer spiders. Here it is the earliest instar that is best fitted for migration on the grounds of size, power and energetics above-mentioned (and see Rogers 1983).

The adult is again typically a migratory stage among vertebrates, but here (Amphibia aside) there is no switch-over between juvenile and adult like that in the insects to a different morph with a different locomotory mode better fitted for migratory specialization, and vertebrates are generally larger and stronger. Accordingly, the immature stages often migrate as well. But departure from the usual insect pattern of a migrant adult and a nonmigrant juvenile goes as far as complete reversal in numerous marine invertebrates. Here the bottom-living adults are non-migratory, whereas the larvae rise (again, apparently phototactically: see Baker 1978, pp. 483–4) and migrate, at any rate in the ecological sense, in the form of plankton on horizontal currents. This rise amounts to "active embarkation on a transporting vehicle." But it surely cannot be assumed to have evolved solely, if at all, as specialized migratory behavior because the medium that transports them also carries the food supply on which they grow: it is their vegetative habitat. They can travel without any inhibition of their vegetative responses.

This is quite untrue of aerial migrants—a point oddly missed by A.C. Hardy when he invented the term "aeroplankton" for the insects that he netted high in the air, although they were entirely out of their habitat for the time being, quite unlike the marine plankton which was his primary concern. Given a habitat that also transports them, the marine animals in question are able to do their migrating as juveniles, often with even less specialization than the small migratory larvae of flightless insects. They undoubtedly migrate in the ecological sense, horizontally as well as vertically. The question of whether they migrate horizontally in the behavioral sense, as well, cannot be given a general answer; it is a matter that requires investigation in each separate case, like nomadism. In some cases they apparently do show specialized migratory behavior, adjusting their level in the water in such a way as to be carried by profitable currents at a certain stage of their development, as already mentioned. Cases where their migration is not accompanied by any inhibition of vegetative responses, however, constitute obvious exceptions to

the "rule" that migratory behavior includes such inhibition. They are exceptions that could be said to "prove the rule" for other migrants whose vegetative habitat is not at the same time a transporting vehicle.

SPATIAL BEHAVIOR AND SPATIAL POPULATION DYNAMICS

Foregoing sections have attempted to illustrate the proposed definition of migration in the behavioral sense as a category distinct from migration in the ecological sense, and of lesser scope. The Taylors have highlighted this distinction and presented a strictly ecological definition of migration: population re-distribution by movement. But their treatment of migratory behavior still seems to confuse the two levels. The definition of migratory behavior proposed here does not refer solely to the movement itself, which varies greatly in mechanism, but invokes also the more constant, negative feature: inhibition of vegetative responses.

Confounding of the ecological and behavioral levels has led students into more and more conceptual and hence terminological difficulties, chronicled by Baker (1978, 1982) and the Taylors (1983). Thus Johnson (1969) concluded from his exhaustive survey of insect migration that definitions of it based only on behavior could be no more than partial, and Baker (1978, p. 18) took this as an early sign of the failure of Johnson's and other entomologists' whole approach to the subject. But that conclusion of Johnson's was the direct result of the vain attempt to find a definition that combined the ecological and behavioral levels as if they were co-extensive and any criteria should apply to both. Dingle (1980) made a fresh attempt to do the same thing, and the result was a bare, noncommittal definition as we have seen. Southwood (1962) had defined insect migration in line with the Oxford English Dictionary definition of "migrate": "to move from one place of abode to another"; but Southwood (1981) agreed with Baker (1978) that defining migration did present problems and refrained from doing so again. Nevertheless he could not accept Baker's very broad definition, and confusion was worse confounded.

Pointing to the existing confusion in terminology and the concepts it conveys, Baker offered an escape from the impasse by means of a "major semantic purge" of the field (1982, p. 7) to accommodate his entirely new view of it which he says is a product of "the behavioural ecology revolution" (1982, pp. 1–4). This refers to evolutionary behavioral ecology which he says is "the new establishment for behavioural theorists" (ibid. p. 1), a "new regime" superseding ethology which saw animals "only as bundles of innate reflexes traveling from one automatic response to another" (ibid., pp. v–vi). Behavioral ecology is on the contrary an "anthropomorphic concept of animals" (p. v). The animal is "a sentient creature attempting as an individual to solve the spatial and temporal problems created for it by its environment" (ibid., p. 14) "in much the same way as Man" (p. v). On this basis, migration is identified with exploratory behavior and defined accordingly as any movement from one place to another.

The argument is bewildering. Neither Tinbergen (1951) as a founder of Ethology nor his scientific descendants have ever regarded the study of the function or "survival value" of behavior (its evolutionary, ultimate causes) and the study of its present (proximate) causes as rival "regimes," one of which could supersede the other as the scientifically legitimate "establishment." The surge of interest in ultimate causes since Hamilton (1964) is not that kind of scientific revolution: the complementary study of proximate causes remains as legitimate and necessary as the evolutionary half of Behavioral Ecology. Nor do ethologists or evolutionary behavioral ecologists (e.g., Krebs and Davies 1981) regard the study of function as anthropomorphism. They would be astonished, too, at Baker's identification of proximately causal ethology with inflexible, push-button reflexology, and would repudiate his charge (Baker 1982, p. 1) that they have "seen an animal as an automaton, a very simple machine." That was precisely the view they have always rejected, from Lorenz (1950) and Tinbergen (1951) through to Halliday and Slater (1983), and have managed to supersede. Indeed Baker has reintroduced the very confusion of approaches that Tinbergen (1951, p. 5) effectively warned them against. Altogether, it seems just as well that there do remain as Baker says (1982, p. 4) some "pockets of resistance" to his revolution.

Maintaining a clear distinction between the behavioral and ecological levels seems to be a better way out of the existing conceptual muddle. It opens the way towards the objective criteria which the Taylors find so deplorably lacking in existing mixed definitions. It should now be possible, for example, to separate out the behavioral content from Southwood's (1981) definition of habitat:

> The area that provides the resource requirements for a discrete phase of an animal's life.
>
> The habitat, as so defined, is also the area traversed by the animal's trivial movements, that is those within its sensory range where it forages.

Note first that "a discrete phase of an animal's life" could be a nonbreeding phase. A habitat is not necessarily vegetative; it can be a non-vegetative, diapause site—the viewpoint taken here but not by the Taylors (p. 500). At the same time this definition of habitat combines criteria from the ecological and behavioral levels, and the Taylors (1983, p. 201) predictably rejected it on account of the "untenable qualifications" added to the ecological content. "Untenable," because they contain "subjectively selected" units such as habitat "for which no criteria can usually be given" (1983, p. 207). Even if no criterion of habitat has usually been given, the question for the future is whether in principle one could be.

In the context of the "spatial dynamics" of populations (to borrow the Taylors' useful term, presumably designed to remind us that "population dynamics" has for too long meant only temporal dynamics), a habitat is a spatial unit, an area (or volume). In the first, environmental or ecological part of Southwood's definition of habitat above, the criterion is the presence of required resources. But as Hassell and Southwood (1978) pointed out, the presence of required resources in an area does not

of itself make that area a spatial unit of habitat. The animal's station-keeping behavior in the presence of those resources is what makes it one. Clearly, the density of the resource items in the area must be sufficient to have that localizing, station-keeping effect, but the criterion still lies in the behavior.

The second part of the definition specifies "trivial" movements within the area as an additional, now behavioral, criterion of habitat. It does not say explicitly that they play any part in delimiting the habitat area; indeed it seems to say that the movements are trivial because required resources elsewhere are beyond the foraging animal's sensory range. This would beg the question of why its foraging is confined to that area, anyway. The answer can only be that the stimuli received from the resources and associated features ***within*** its sensory range, within the area, keep its movements trivial. Their triviality, meaning small range, will act together with any repellent effects of stimuli from non-resource features, to keep the animal within the area and thereby set the bounds of the area as a spatial unit of habitat.

Thus the first, ecological part of Southwood's definition of habitat depends entirely on the second, behavioral part. This is precisely the Taylors' complaint, but all it means is that the criterion of a habitat as a spatial unit lies at the behavioral rather than the ecological level. A given area becomes a habitat only because it does trivialize the animals' movements. But "trivial movement" in turn lacks an objective criterion or even quantification. Nor do we know how in practice these movements add up to station-keeping and thus turn the area into a trap. The idea of trivial movement as opposed to migration goes back to the turn of the century (for this history, see Johnson 1969, Taylor and Taylor 1983), and yet in all these years there seem to have been remarkably few attempts to quantify the spatial pattern of trivial movements in the field, let alone identify the causal mechanisms.

The recent extensive descriptions and modeling of foraging behavior have been directed to the temporal rather than the spatial patterning of movements within the habitat. Spatial considerations including turning responses have received some attention, notably in Hassell and May (1974), but the purpose of these studies has been to answer questions about population stability over time (Hassell and May 1973, Hassell 1978, Hassell and Southwood 1978) or evolutionary, "ultimate" questions about the allocation of time between more and less rewarding patches of the habitat (Krebs and Davies 1978, 1981). Moreover foraging movements are only part of the behavioral system that makes the habitat area a trap. Reactions to other resources such as conspecifics, shelter, resting places, mating places, learned landmarks, etc., all add to the trapping effect.

What is needed for the purposes of quantifying spatial dynamics is the recording and analysis of the patterns of actual tracks in the field. Those in an area that has been identified as a habitat (as distinct from territorial or other subunits of habitat) on other criteria—population density, presence of resources—need to be compared with those in adjacent nonhabitat areas. No such information is to be found in ecology textbooks and symposia; the need for it was probably not felt so long as "population dynamics" neglected spatial dynamics. This lacuna is confirmed by the lack of any techniques for recording these tracks in the field and analyzing them afterwards, in

"the ecologist's Bible," Southwood's (1978) ***Ecological Methods***. No doubt there are more cases in the literature, but I have come across just six published attempts to make such field measurements ***comparing habitats with nonhabitats*** (not just rich and poor parts of the habitat): two on birds (Smith 1974, 1977) and four on insects (Smit 1960, Douwes 1968, Zalucki and Kitching 1982, Kennedy 1939). Much more is needed in order to quantify spatial dynamics and understand its mechanisms.

The type of spatial maneuver best known to ecologists as a station-keeping mechanism, is ***klinokinesis***, where the reaction is a change simply in the rate or frequency of self-steered turning (Havukkala 1980, 1984; Havukkala and Kennedy 1984). But klinokinesis figures large in the literature of population ecology in only one of its variety of forms: the temporary increase of turning by a parasite or predator after it has contacted and "handled" a host or prey (Hassell and May 1974, Hassell and Southwood 1978, Hassell 1978, Roitberg et al. 1982). The result of this is closer scanning of the immediate vicinity, the ***area-restricted search*** of Tinbergen, Impekoven and Franck (1967). This in turn causes aggregation of the animals on a local patch where hosts or prey are concentrated within the larger habitat. The reaction has a small-scale, short-term (up to minutes) station-keeping effect on the individual, but frequent contacts prolong it. Perhaps more important for station-keeping on the habitat scale is the ***orthokinetic*** arresting effect of meeting many hosts or prey, both the literal arrest while "handling" each resource item and virtual arrestment through the reduction of each intervening bout of locomotory activity (e.g., Zach and Falls 1958, Thomas 1974, Waddington and Heinrich 1981, Kennedy 1966 et ante).

However, there are also other forms of the klinokinetic reaction, some of which operate on a larger scale than that well-known klinokinetic after-effect of direct contact with a resource item, the aggregating consequence of which in any case depends on how much these items are themselves aggregated (Murdie and Hassell 1973, Eveleigh and Chant 1982, Waage 1983). Diffuse stimuli such as odors or air humidity can increase turning without any interruption of the locomotion (see Bell and Tobin 1982, Kennedy 1978, Havukkala 1985, Havukkala and Kennedy 1984). Moreover the sudden cessation of such stimuli from a patch or habitat when an animal moves out can cause it to turn more, and even to turn directly back into it (ibid.). But these unlearned, self-steered reactions that help to trap the animal in any habitat area are overlaid by reactions to features specific to a given area, especially but by no means only in vertebrates. The latter are learned during exploratory behavior and have a similar trapping effect in a habitat, home range or territory. This important learned component is thoroughly documented in Baker's (1978) survey and constitutes what he calls the animal's "sense of location." The station-keeping effect of all these turning reactions to resource-associated stimuli is of special interest for spatial population dynamics because they are all evidently more or less inhibited when the straightened-out movement characteristic of migratory behavior supervenes.

It would be an illuminating exercise to tease apart all these station-keeping responses in the field in specific cases, but perhaps not a necessary one for the immediate end in view. That would be to establish quantitative movement-pattern criteria which will distinguish station-keeping behavior from migratory behavior, and migratory behavior from re-distributive movements during nonmigratory, "trivial" behavior—expecting no hard-and-fast categories, but looking out for bimodalities. Along these lines there may be some hope of finding objective behavioral criteria for the presently vague but ecologically necessary categories of habitat, trivial movement, foraging, station-keeping, etc.—and, of course, for their obverses which make up the subject of migration.

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MIGRATION AND LIFE HISTORIES

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ABSTRACT

Migration confers flexibility on life histories and allows choices of where and when to breed. It thus has profound influences on life history "strategies." Genetic and phenotypic studies of a number of insects suggest the possibility of distinct migration—life history syndromes programmed by natural selection and involving positive correlations among migratory characteristics and aspects of reproduction and survival. The correlation structure suggests adaptation for colonization. In fish there is also evidence for migration syndromes which include reproductive characters, and these may evolve relatively rapidly. In birds there is evidence for considerable genetic variation in dispersal and reproductive characters indicating that correlation structures would be worth investigating. The variation seen in migratory patterns in general can best be understood in the context of the genetic and phenotypic "architecture" of life histories.

INTRODUCTION

Migration is an important component of the life histories of many organisms as the papers in this symposium attest. Not only does it permit escape from unfavorable conditions, but it also allows exploitation of habitats created by successional, seasonal or, as in the case of plankton, even daily changes in the environment. The migrant can thus make use of resources patchy in space and time and determine via its behavior where and when to breed. The latter in turn involves reproduction and survival and hence fitness. The advantage of migration to fitness can be considerable (Solbreck, this volume). It is this relationship between migration and life histories that I wish to explore here. The problem is an important one because the involvement with fitness places the study of migration–life history "strategies" directly in the mainstream of evolutionary biology (Bell 1980; Dingle 1984, in press).

The question I shall address is just how the relationship between migration and other life history traits is constructed to form a "strategy." Specifically we wish to know if there is a characterizable migration–life history syndrome (or syndromes) with identifiable sets of connections among the relevant ecological, physiological and genetic factors. Such connections would imply a complex adaptation (Frazetta 1975)

with traits tied together and organized to make the adaptation function appropriately. The presence of such a complex adaptation is implied by Kennedy (1961, 1975 and this volume) when he identifies migration as specialized behavior involving the enhancement of locomotory reflexes which temporarily inhibit "station-keeping" responses, i.e., those involved in keeping the organism in the habitat where it feeds and reproduces, but promote their later recurrence. Rankin and Herman (this volume) have documented the hormonal control of this physiological syndrome in very diverse insects, and Meier and Fivizzani (1980) have discussed the association between reproductive hormones and migration in birds. Physiological ties between migration and life histories are thus established. I shall therefore concentrate here on ecology and genetics and review some of the ways these might influence migration and life cycle patterns.

A life cycle syndrome which includes migration would be expected to display certain attributes. Since migration allows escape from uncertain or unfavorable habitats and the colonization of favorable ones, selection should produce a suite of life history traits that coevolve with migratory behavior to promote (1) flexibility in the face of uncertainty and (2) the ability to successfully colonize (Safriel and Ritte 1980, Simberloff 1981, Dingle 1984). Such a suite might include larger size which seems to be selected for when environments are heterogeneous (Roff 1978; Dingle, Blakley and Miller 1980; Fairbairn 1984), more rapid development to adulthood to minimize the possibility of being trapped in a poor habitat, the potential for early reproduction in the new habitat, higher fecundity to further promote colonization, and appropriate life history responses to environmental cues which signal changing conditions. A good example of the latter is photoperiod. The molding of suites into adaptive syndromes by selection requires that the traits be organized genetically by the appropriate sets of genetic correlations (Hegmann and Dingle 1982, Rose 1983, Dingle 1984). A reasonable prediction concerning the above traits would be an array of positive genetic correlations tying them together into a migration–life history strategy or syndrome. In this paper I shall survey data relevant to this prediction and to the relationship between migration and other life history characters which promote flexibility such as diapause and wing polymorphism. Most of the data will be from insects because they have proved the most amenable to studies of migration and life histories, but I shall also consider some selected vertebrates and try to point out directions further studies might take.

MIGRATION AND DIAPAUSE

Many insects which breed in the temperate zone overwinter by entering a state of developmental arrest known as diapause which is usually cued by photoperiod. In some species such as the coccinellid beetle *Hippodamia convergens* there may also be a quiescent period over a summer dry season. In either case the inactive state is passed in a protected site, and there are often migratory movements to and from such sites so that migration and diapause combine for added life cycle flexibility. These movements may be quite local or, as in the case of *Hippodamia* (Hagen 1962), the

milkweed bug ***Oncopeltus fasciatus*** (Dingle 1978) and the monarch butterfly ***Danaus plexippus***, they may cover considerable distances. The extreme case of migration to a diapause site is that of the northeastern North American population of the monarch butterfly which may migrate several thousands of kilometers to overwinter in the volcanic plateau of central Mexico (Brower, this volume).

Whether movement occurs over short or long distances, the pattern of the migration-diapause relationship is generally similar. An example is the well-studied case of the seed bug ***Lygaeus equestris*** on the Baltic island of Gotland (Solbreck 1972, 1976, this volume; Solbreck and Sillèn-Tullberg 1981). In the fall, adults migrate to diapause sites in sheltered rock out-croppings and around stone buildings. During the overwintering period, energy is provided from an enlarged fat body which shrinks as reserves are metabolized, and the ovaries are undeveloped. As the winter progresses, the insects become more susceptible to stimulation of the reproductive system by warm temperatures, and diapause is essentially ended by January with the insects remaining dormant as a consequence of the extreme cold. The bugs also become more sensitive to stimuli inducing flight as has also been found in the ladybird beetle ***Coleomegilla maculata*** (Solbreck 1974). With spring warming in May, there is emergence from the diapause site and migration to host plants in the surrounding terrain. Under the stimulus of feeding, the ovaries mature, and the bugs produce the new generation which will diapause the following winter, although in warm years a partial second generation can be produced. The "decision" to diapause involves a delay in reproduction but results in the benefit of winter survival. There are thus life-cycle trade-offs which involve migration, diapause and reproduction.

A direct relationship between migration and diapause has been demonstrated for the milkweed bug ***Oncopeltus fasciatus*** (Dingle 1978). Like the monarch butterfly, ***O. fasciatus*** invades northern latitudes in the spring and produces up to three summer generations depending on location and climate. The bugs are unable to tolerate temperate zone winters with long periods of subfreezing temperatures; rather, the evidence suggests that they return south (Dingle 1981). This return movement is facilitated by a short-day diapause which occurs in the adult (Dingle 1974) and results in the cessation of reproduction. Using tethered flight, we have demonstrated that the bugs can migrate throughout the diapause period, whereas under summer conditions, migration ceases 2–3 weeks after adult eclosion when reproduction is initiated (Dingle 1978). Diapause may last 60 days or more at 23°C, giving the insects ample time to migrate considerable distances. As with the monarch butterfly and ***L. equestris***, migration and diapause result in delayed reproduction, but with the alternative gain of escape to more favorable conditions for overwintering (and in ***O. fasciatus***, reproduction). The monarch and ***O. fasciatus*** are each the only members of tropical groups to invade the temperate zone, and it seems likely that the evolution of a migration-diapause system made this possible (Tauber and Tauber 1976; Dingle 1978; Brower, this volume). If so, this is an important link between the two behaviors and further emphasizes the importance of overall life-history pattern.

A further case of an intimate relation between an adult reproductive diapause and migration occurs in the cotton stainer bugs *Dysdercus* spp. which migrate entirely within the tropics. These insects feed on the seeds of various Malvales and undertake migrations to exploit seasonally available resources, usually at the beginning of the dry season (Dingle and Arora 1973; Derr 1980a, b; Dingle 1982). Migrations occur during periods of food or water shortage, when females delay reproduction (diapause) and retain wing muscles; when a suitable host plant with ripe seeds is found, feeding commences, wing muscles are histolyzed and egg development is initiated. The more migratory species are larger and show more rapid early reproduction (Derr, Alden and Dingle 1981) which suggests a life history strategy adapted for colonization.

The nature of life history variation in the New World *Dysdercus bimaculatus* was examined by Derr (1980b) under conditions of plentiful food and water and under water stress. The latter was chosen as an environmental variable, since water is necessary for feeding in these seed-sucking bugs, and its availability determines whether the bugs migrate or histolyze wing muscles and reproduce locally. The level of environmental moisture stress varies among the host trees (*Sterculia*), and response to stress varies among females. Individuals thus face considerable uncertainty and a number of options for reproduction in time and space. In the nonstressful environment, heritability estimates for characters having to do with timing (age at first reproduction, inter-clutch interval) were not significantly different from zero, while those relating to fecundity (e.g., clutch size) were estimated at around 0.30 (i.e., about 30% of the variance for the trait was additive genetic variance or that variance contributing directly to parent-offspring resemblance and hence sensitive to selection). In the stressful and more uncertain environment, heritability for age at first reproduction was also around 0.30; in contrast to favorable environments, the environmental uncertainty associated with water stress seemed to maintain greater additive genetic variance. Even more interesting, age at first reproduction was not associated with other life history traits in any predictable way; division of the females into early and late reproducers did not result in division on the basis of any other traits. I shall return to this lack of association between age at first reproduction and other life history traits below. It will suffice to note here that the association between the starvation diapause of *Dysdercus* and migration involves both phenotypic and genetic complexity (see review in Dingle 1984).

MIGRATION AND WING FORM

Many insects have evolved wing polymorphism (genetic) or wing polyphenism (environmental) in response to habitat variation (see Dingle 1980 for review and Zera, this volume, for a discussion of the genetics). In general, species or populations from isolated sites (e.g., mountaintops, bogs) and lusher more stable habitats are brachypterous or apterous, while those from harsher or more temporary conditions are macropterous. In a well-studied example, Vepsäläinen (1978) has shown that European gerrid bugs (Hemiptera: Gerridae) run the gamut from fully winged to wingless with a range of intermediate populations and species displaying polymorphic

and/or polyphenic combinations. An interesting exception to the general rule seems to be the absence of wing morph variation in many of the temperate zone arboreal phytophagous Hemiptera (Waloff 1983). These are fully winged even in lush permanent habitats, probably because flight provides the most efficient locomotory mechanism for moving about in trees, which are large and architecturally complex.

The advantage of flight to escape unfavorable habitats and to colonize favorable ones is obvious, but what are the advantages of winglessness given that it forces the insect to remain sedentary? The reasonable consensus seems to be that in the absence of wings and associated flight muscles, more energy can be channeled to reproduction (see also Zera, this volume). The occurrence of post-flight wing muscle histolysis in many species is consistent with this view. For some species, however, the evidence is not always obvious. Denno (this volume), for example, finds little difference in the life histories of the two morphs of the planthopper ***Prokelisia marginata***, and there are similar results from other insects (Dingle 1982).

In the species where there is reproductive benefit, this seems to take two forms (Dingle 1982; Zera, this volume). First, flightless individuals are more fecund, and secondly, they also reproduce earlier (note that there is some tendency for earlier reproduction in Denno's ***Prokelisia***). The latter trait especially allows more rapid population growth and a greater contribution by the individual female to future generations (Stearns 1976). An example of the generally greater fecundity of apterous aphids is shown in Figure 1 which compares morphs in ***Sitobion avenae*** and ***Metapolophium dirhodum*** studied by Wratten (1977). In both cases, there is greater production of nymphs by apterae of these viviparous aphids across all age classes. Apterae tend to be larger than alates, but the differences hold even when the data are corrected for size. In some cases apterae can produce almost double the number of young when compared to alates, so that production of alates does indeed involve life history trade-offs.

In aphids the switch to alate production generally results from crowding and is thus an environmental effect. But in the pea aphid ***Acyrthosiphon pisum*** (Lamb and MacKay 1979) and undoubtedly others, there are genetic influences which arise from differences among clones. These differences occur in the proportion of winged forms produced under a standard crowding stimulus. Clones sampled from the periphery of alfalfa fields or from isolated fields produced a smaller proportion of alates than those sampled from the centers of fields, probably because they lost more migrants than they received. Clonal differences were consistent across generations. The varying degrees of selection for migration on aphid clones produce populations that are both genetically and phenotypically flexible with respect to migration, and the two morphs provide specialization for the productive and migratory aspects of life histories, respectively. Similar strategies are also evident in other wing polymorphic or polyphenic insects (Dingle 1982).

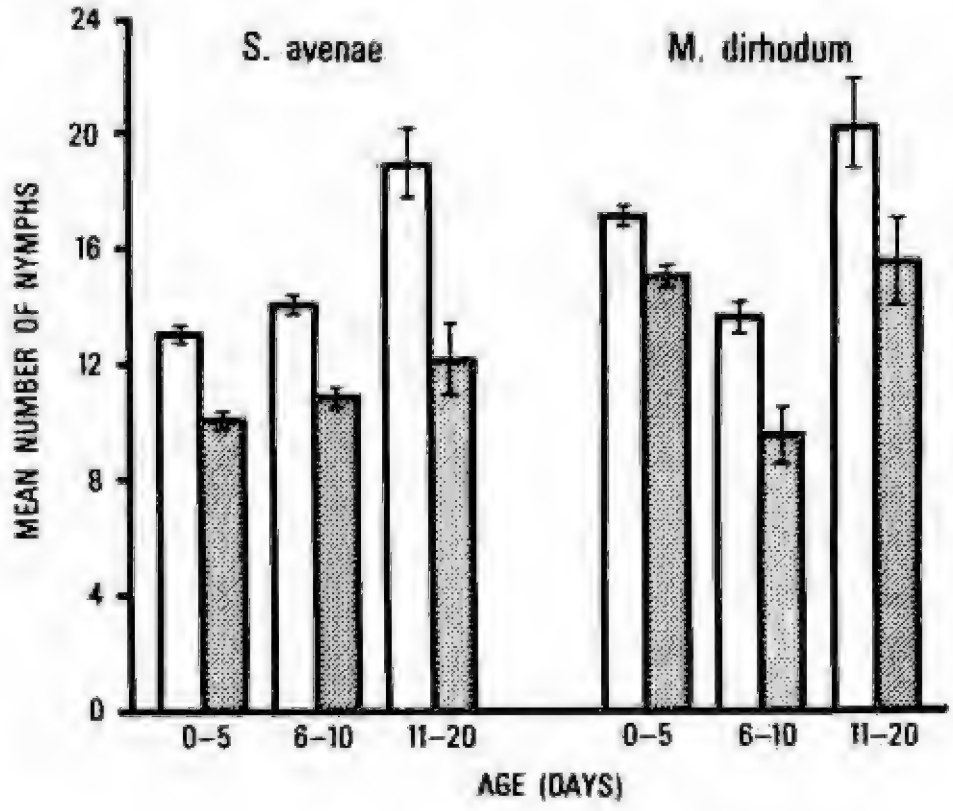

Figure 1

Reproduction (means ± s.e.) in the aphids *Sitobion avenae* and *Metapolophium dirhodum* over the major portion of adult life. Open bars are apterae, hatched bars alatae. Note greater nymph production by apterae of both species. Data from Wratten (1977).

MIGRATION–LIFE HISTORY SYNDROMES

Since migration is likely to involve colonization of new habitats (or empty habitats in the case of return to breeding areas), selection should produce complex adaptations which include both the ability to migrate and the ability to colonize, and which persist in the new environment (Simberloff 1981). The life history characters which best promote colonization and persistence are early and rapid reproduction (Safriel and Ritte 1980), and indeed migrant colonizers are often described as "*r*-selected" as a consequence of these characteristics (Stearns 1976). These traits are phenotypically correlated with migration, but the important issue for evolutionary biologists is the extent to which the phenotypic correlations contributing to successful colonization are genetically based (Dingle 1984, in press).

We (Hegmann and Dingle 1982) undertook a three year study of half-sib and full-sib families in milkweed bugs (*Oncopeltus fasciatus*) to examine this issue. The genetic correlation matrix resulting from that study indicated strong positive genetic correlations among size, fecundity, and development rates. In other words the syndrome of large, rapidly developing and fecund bugs was based on genes shared by these traits. A further interesting result was the failure to demonstrate a correlation between age at first reproduction and any of the other characters (see Derr's results for *Dysdercus* discussed above). The follow-up study, using selection for wing length to assess genetic correlation structure, is reported by Palmer elsewhere in this volume. Palmer's results confirm the results of the sib-analysis and also demonstrate a positive genetic correlation between flight and the size and fecundity measures, supporting

predictions concerning a migration-life history syndrome.

A life history syndrome involving migration has similarly been demonstrated in ***Tribolium castaneum*** by Lavie and Ritte (1978) and Wu (1981). They used movement between vials of flour in laboratory experiments as an index of migration ("dispersal" in their terminology). In both cases "dispersing" and "nondispersing" lines of beetles were generated by selection and examined for correlated life history traits. The summary of the results in Table 1 clearly shows the existence of positive correlations between migration and production characteristics as might be expected for colonizers. The "high dispersal" line consisted of larger beetles which produced more and larger eggs after developing more rapidly. Wu also selected successfully for high and low "dispersal" in the related *T. confusum*, a more sedentary species. In the latter case Wu was unable to demonstrate positive correlations between production and migration, suggesting that the colonization syndrome was characteristic only of the more migratory species, *T. castaneum*.

The migration-colonization syndrome in some insects may also involve a direct influence of flight on reproduction (Dingle 1985). In alates of the black bean aphid ***Aphis fabae*** for example, flight induces settling and larvi-position responses (Kennedy and Booth 1963a, b). In this species reproduction by alates is greatly delayed if no flight occurs. In the frit fly ***Oscinella frit***, flight shortened the pre-oviposition period by as much as three days, with the effect more pronounced in younger females (Rygg 1966). Similarly the pre-oviposition period was shortened by approximately five days in ***Oncopeltus fasciatus*** by bouts of tethered flight (Slansky 1980). In an interesting experimental study of the relation between wing polymorphism and egg production in the cricket ***Pteronemobius taprobanensis***, Tanaka (1976) found that micropters began laying eggs earlier and produced more eggs than macropters. But macropters of this insect frequently lose the wings after flight. Tanaka also found that artificially de-alating macropters resulted in increased egg production. There is thus apparently feedback from the wing form to the ovary, although just how this is mediated remains to be discovered. Suffice to say that there is a significant behavior component (phenotypic) to the enhanced reproduction that occurs in migratory populations or species.

VERTEBRATE MIGRATION AND LIFE HISTORIES

With their relatively large sizes and long generation times, vertebrates have not proved as amenable to the study of migration-life history patterns as have insects, but there has been considerable recent progress (reviewed in Dingle 1980). This progress has been most evident in studies of fish and some of the important current work is summarized in papers in this volume (e.g., Dodson, Leggett, Quinn). Fish migration from the sea to fresh water rivers in particular is apt to involve considerable energy expenditure with concomitant trade-offs which involve reproduction. Schaffer and Elson (1975) examined migration in the Atlantic salmon (***Salmo salar***) from an energetic and life history perspective and made several predictions. The first of these was that long, fast rivers in which high energy expenditure is required to reach

Table 1

Comparison of life history traits in the flour beetle ***Tribolium castaneum*** between lines selected for high and low migration rates. Data from Wu (1981); egg production data from Lavie and Ritte (1978). All differences between lines are statistically significant.

Character	High migration line	Low migration line
Migration rate[1]	6.83	1.59
Development time[2]	29.03	30.51
Egg production in 4 day period	47.8 ± 1.8	42.2 ± 1.8
Egg length (mm)	0.601	0.586
Body weight (mg)	22.6	19.7

[1] Mean number of vials traversed in generation 17
[2] Median number of days from egg to adult

spawning grounds would select for a longer feeding period at sea to provide energy for the spawning run and delayed reproduction as a consequence. Secondly, they predicted that rapid growth at sea subsequent to the age at first possible spawning (increased growth and future return per unit effort) should be characterized by relatively delayed spawning. Finally, high year-to-year variation in juvenile survival should result in selection for adults spawning at different ages, i.e., individuals should "bet-hedge" by producing offspring with high variances for age at first reproduction. These predictions generally held for rivers in eastern Canada and demonstrated the importance of phenotypic correlations between migration and life table characters.

Life histories with respect to migration have also been studied in the American shad ***Alosa sapidissima*** (Carscadden and Leggett 1975, Shoubridge 1977). In the St. John's River in Florida, environmental variance is low with relatively high temperatures optimal for juvenile survival over a long period. The high temperatures are, however, a stress for adults because they result in high energy expenditure during the upriver spawning migration. This population is semelparous with a high fecundity of 412,000 eggs per spawning. In contrast in the Miramichi River in New Brunswick, environmental variance is high and the generally low temperatures reduce the energetic cost of migration but increase mortality of juveniles. Here iteroparity is the rule with delayed age at first reproduction and total fecundities of only some 266,000 eggs per lifetime. Variation was also noted as a function of river length; longer rivers create greater risks for adults and tend to select for semelparity. Long Pacific rivers may have been a major factor selecting for the general pattern of semelparity seen in Pacific salmon (*Oncorhynchus* spp.; see also Quinn, this volume).

Table 2
Life histories of migratory shad (*Alosa sapidissima*) in North American rivers. Data from Shoubridge (1977).

Region	Ratio Adult/Juvenile Survival	Reproduction	Environmental Variance*	Maturity	Fecundity
North Atlantic	High	Iteroparous	High	Delayed	Low
South Atlantic	Low	Semelparous	Low	Early	High
Pacific (Introduced)	High	Iteroparous	Low	Early	High

*Primary effect is on juvenile survival

On the west coast of North America, shad were introduced in the late 19th century, and there has been rapid evolution of migration and life history patterns. These shad came from the Hudson, Potomac and Susquehanna Rivers where 20 to 40% of the adults are repeat spawners, age at maturity is about 4 years for males and 4.6 years for females, and lifetime fecundity is on the order of 300,000 to 350,000 eggs. The Pacific Rivers where these fish were introduced display a much wider range of conditions, reflected in the life histories of the respective populations. Here 32 to 77% of the females are repeat spawners, age at maturity is from 3.3 to 3.8 years for males and 4.0 to 4.5 for females, and lifetime fecundities range from 321,000 to 500,000 eggs. The life histories of Atlantic and Pacific shad are briefly compared in Table 2. The rapid evolution of differences suggests strong local selection pressures and considerable genetic variance for the traits. We do not know the extent of possible genetic, developmental or environmental correlations, and these would be well worth studying.

There are also some recent efforts to analyze bird migration and its relation to life histories. Andersson (1980) examined the occurrence of nomadism which he defined as the tendency for both adults and juveniles to wander widely in search of food and for the adults to settle and breed where food is locally abundant. This behavior contrasts to the more usual case where breeding occurs at the same location from year to year. Both theoretical considerations and empirical data suggest that nomadism is more likely with cyclic rather than random fluctuations in food abundance. Given cyclic food production, nomadism is favored in birds with large clutches and a higher ratio of juvenile to adult survival. Birds with large clutches also tend to mature earlier and the combination of the two factors constitutes a good colonization "strategy," as described above for insects. The pattern is characteristic of, for example, snowy owls which also depend on cyclic food resources (lemmings) and are well known for their irruptive movements. A summary of Andersson's

Table 3
Factors favoring adult nomadism in birds (after Andersson 1980).

Factors	Examples
Cyclic resource fluctuation	High arctic, Australian deserts
Long intervals between good years	Seed crops of boreal trees
High Juvenile : adult survival ratio	
Large clutches	Snowy and short-eared owls 8–10 eggs) vs. jaegers (2 eggs)

conclusions, with some examples, is given in Table 3.

A second example from bird life histories comes from long-term studies of populations of the European great tit (*Parus major*) in England and Holland (summarized in Table 4). These populations were nonmigratory, but the young do disperse to breed away from the territories on which they were raised. Heritability estimates of an array of life history traits (Table 4) indicate relatively high proportions of additive genetic variance, suggesting that these traits would respond quite rapidly to selection. About 60% of the variance for dispersal, for example, is the result of additive genetic influences; offspring, in other words, display dispersal patterns very similar to those of their parents. As in the case of fish discussed above, what we do not know is the genetic correlation structure. However, the heritability estimates certainly suggest that they would repay study. Are the high genetic variances observed (see also Berthold, this volume) associated with high genetic covariances? If so, which traits are involved, and does the covariance structure suggest a life history–dispersal syndrome (in the tits) or a migration–life history syndrome in migrants? If the insect data are any guide, we might predict a positive association between migration and clutch size (see also Andersson's analysis in Table 3) since this would be a good colonizing strategy, but no association between migration and onset of laying, indicating behavioral flexibility in the face of environmental variance (see below). Data on the extent of these covariances should give a new perspective to the "why" questions of bird migration (Dingle 1980). The apparent presence of large genetic components of migratory behavior in "true" migrants (Biebach 1983; Berthold, this volume) suggests that questions about migratory strategies in birds, although by no means easy to answer, are now tractable.

Similar studies of life history syndromes should also be profitable with small mammals. Certainly there is a genetic component to dispersal behavior (Krebs, Gaínes, Keller, Myers and Tamarin 1973; Rasmuson, Rasmuson and Nygren 1977), and life history differences occur between migratory ("dispersing") and nonmigratory populations (Sullivan 1977; Tamarin 1977a,b). For a full analysis, what we now need to know is whether the phenotypic associations have a basis in a genetic correlation structure.

Table 4
Heritability estimates for various life history traits in British and Dutch populations of the great tit (*Parus major*).

Trait	Heritability (h^2)	Source
Body weight	0.59–0.72	van Noordwijk et al. 1980
Clutch size	0.37–0.38	van Noordwijk et al. 1980
	0.48	Perrins and Jones 1974
Onset of laying	0.14	Jones 1973
	0.30	van Noordwijk et al. 1980
	0.18–0.45	van Noordwijk et al. 1981
Dispersal distance	0.56–0.62	Greenwood et al. 1979

DISCUSSION AND CONCLUSIONS

The importance of migration to life histories means that a complete understanding of ***why*** animals migrate must place migratory behavior in the context of overall fitness. This in turn means consideration of reproduction and survival characteristics associated with migration. The data I have cited imply that the association may have a particular structure based on an array of genetic and phenotypic correlations with other traits of the life history. The net result is a "syndrome" or "strategy" adapted, within the constraints imposed by environment, development and phylogeny, for migration and colonization. Migration brings flexibility to life histories and fitness functions and is important to the continuum which connects proximate and ultimate aspects of adaptation (Leggett, this volume).

The evolution of migration strategies depends on both the environment, which determines selection pressures, and on the underlying genetic and developmental structures, which determine the response to selection. While not ignoring the former, my focus here has been on the latter. The presence of significant components of additive genetic variance for migration and life history traits, e.g., Table 4, indicates that considerable response to selection in these traits is possible. But more importantly, genetic correlations among traits, e.g., Table 1 and Palmer (this volume), indicate that responses do not occur in isolation, but rather that selection on one trait can also result in responses in others. In other words clusters of traits will evolve together producing complex adaptations or "strategies." I have focused on correlations with life histories, but there are other potentially important correlations as well. What, for example, is the genetic basis for orientation and navigation, and does it contribute to the structure of migration syndromes as outlined here?

One particularly interesting aspect of insect life history strategies revealed by the available studies is the apparent lack of correlation between age at first reproduction and other traits as seen in *Oncopeltus* (Hegmann and Dingle 1982, Dingle 1984) and *Dysdercus* (Derr 1980b). Age at first reproduction (α) has repeatedly been shown to

display high proportions of additive genetic variance in uncertain environments (review in Dingle 1984) allowing a range of responses which function like a "genetic rheostat" (Dingle, Brown and Hegmann 1977). To understand why a good migration strategy might not include correlation of a variable α with other traits, consider the consequences of strong genetic correlations. If these were present, variation in α could cause detrimental variation in the traits with which it was correlated (whether positively or negatively). Conversely, α might be prevented from varying (and hence from responding flexibly) if a large negative correlation with another character made it impossible for natural selection to alter both in the same direction. This would represent a cost in terms of flexibility (a "cost of correlation"), and might select for independence of α from other traits. A number of traits such as the timing of migratory movement might similarly be independent. The possible generality of such relationships across taxa seems very much an area ripe for investigation. These points are elaborated further in Dingle (1984).

A second interesting aspect of insect life histories is the maintenance of wing polymorphism. In the usual situation apterous or brachypterous morphs of low mobility and high reproductive potential are present under stable conditions, while macropterous forms of high mortality and lower reproductive performance serve for migration to different habitats when conditions deteriorate. Life cycle trade-offs are partitioned between the morphs. Gene differences occur in the thresholds for wing production (Lamb and McKay 1979; Zera, this volume), but we know essentially nothing of the association of thresholds with other life history traits either phenotypically or genetically. Are there, for example, trait associations with low threshold for macroptery similar to associations between migration and life history characters in other insects (e.g., *Oncopeltus*), or are there differences in the wing polymorphic species? The presence of such clear alternative strategies would seem to make insects particularly attractive organisms for probing the "why questions" of migration.

An important task for the evolutionary ecologist is the determination of the structure or "architecture" of genetic and phenotypic correlations and the prediction of the course evolution will take. Studies of migration are thus fertile fields for analysis of important evolutionary questions as I suggested at the beginning of this paper. It is a mark of our progress in studies of migration that the questions have been defined; it is a measure of our task that their analysis has barely begun.

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CHAPTER ONE

PLANKTON MIGRATIONS

The ability of many zooplankton species to regulate their vertical distribution is a striking feature of pelagic communities. Attention has focused more on the daily cycle of movement in and out of the near-surface layers of pond, lake and ocean, than on the longer scale movements involving seasonal or ontogenetic migrations. In an environment full of physical features with scales of events ranging from eddy-diffusion to mesoscale eddies or ocean-wide current systems, it would be unexpected if organisms were found not to have evolved behavioral responses which allow them to exploit the dynamics of the physical structure of the water within the limits of their physical capabilities. Thus an oceanic copepod capable of vertical migration rates of 100 m per hour may well also be able to regulate its horizontal distribution within features with scales of 10^2 m, scales that are within the sampling scales achievable with multiple-serial samplers.

Marine animals perform migrations in response to vertical gradients of various types, and the effects on biogeochemical cycles can be significant. Angel explores the limits to and probable causes of migrations by oceanic zooplankton and nekton in both the vertical and horizontal dimensions and for both diel and longer time scales. He then presents possible biological and geochemical implications of such behaviors. Throughout his paper, Angel refers to both the literature and results of his Department's recent investigations.

After initially describing migrations, determining which species are involved and what are the extent and timing of their movements, planktonologists have tended to concentrate on the question of why they do it. Kerfoot reviews the four main hypotheses which address the adaptive significance of the migrations. He concludes that response to cyclic variations in predation pressure correlated with the light cycle combined with the gradients in resource availability will make diel vertical migrations one important solution to the problems of successful survival in the pelagic environment.

Some progress can be made in testing such hypotheses and in exploring other aspects of the ecological significance of migrations to the individual animal, to each species and to the community in general, by field observations. Major progress will only be achieved by careful and well-designed experiments. Huntley, in reviewing experimental approaches to migration in plankton, has shown how limited they have been in clarifying our understanding, mainly because of the problems of adequately duplicating real physical environments and resolving ways of elucidating the synergistic influence of depth-related factors. But he emphasizes just how important it is for planktonologists to continue to strive to devise effective methods of manipulating natural and artificial pelagic ecosystems. Planktonic migration is an essential element in pelagic ecology and continues to present a major intellectual and

technical challenge to both oceanographer and limnologist.

It may seem unlikely that microscopic plants (phytoplankton) can undertake vertical migrations in apparently turbulent lakes and oceans. Nevertheless, these environments are not always well-mixed by waves and currents and are usually thermally stratified for considerable periods of the year. Under such circumstances of low mixing, phytoplankton can move at speeds greater than the velocities of the surrounding water masses and so be capable of depth-regulation or migrations.

Phytoplankton consists of communities of organisms of diverse morphology, size and taxonomic group. Algal species exist as cells ranging in maximum dimension from about 1 μm to hundreds of micrometers, and the cells may be single or colonial. Vertical movements may be due to (1) sinking as, for example, with diatoms, (2) sinking or floating due to controlled changes of buoyancy, best observed in the blue-green algae or Cyanobacteria as they are now known, and (3) active swimming by algae possessing flagellae. Rates of movement between species vary from negligible to nearly four meters per hour. The combination of different mechanisms of motility together with the wide range of cell size, morphology and rate of movement give rise to a rich variety of vertical migrations within the phytoplankton.

Algal cells generally endeavor to grow whenever and wherever possible. To do so they require an adequate supply of light and nutrients. However, phytoplankton growth usually results in the flux relative to need of a major nutrient or energy becoming insufficient, and strong vertical gradients of light and nutrient concentrations become established. Vertical movements or depth-regulation by different algal species then can play an important role in controlling their relative success. Migrations can thus be considered as a means for enabling cells to move into positions conducive for growth or, of equal importance, avoiding deleterious conditions. As algal species have different nutritional requirements; what may be suitable conditions for growth for one species may be harmful for another.

The papers in this section of the symposium discuss and give examples of various algal migrations common to lakes and oceans. One paper (Heaney and Butterwick) compares and contrasts different mechanisms of movement and their possible significance for phytoplankton growth. The other papers deal with specialized studies and reviews of migrations of particular algal groups or species. These include two accounts of factors regulating dinoflagellate migrations, one concerning temperature (Kamykowski) and the other biochemical control (Cullen). Over the last 15 years much has been learned about migrations of the Cyanobacteria and this is reviewed and some experimental results presented (Klemer). Some experiments on migrations by the ubiquitous but poorly studied Cryptophyceae are described by Sommer. It is hoped that these studies will provide an interesting stimulus to research on phytoplankton dynamics and perhaps also to others who have a curiosity to know what goes on "below the waves."

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VERTICAL MIGRATIONS IN THE OCEANIC REALM: POSSIBLE CAUSES AND PROBABLE EFFECTS

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ABSTRACT

Oceanic organisms live within an environment that is dominated by vertical gradients—gradients in availability of food, nutrients, light, predation pressure and current shear. These gradients vary both in time (e.g., seasonally) and in space (e.g., latitudinally). Each organism is faced with the often conflicting need to survive, feed, breed, and to optimize its use of the available resources. Unless an organism is large enough either to avoid the gradation in predation pressure through sheer size or is mobile enough to be able to exploit large space scale variability by extensive horizontal migration (e.g., as seen in the large whales), for most oceanic organisms an important "option" will be a cycle of vertical movement.

The connotations of this "option" will be discussed. Migrations may feed back into environmental processes that are important not only biologically but also geochemically.

INTRODUCTION

Oceanic animals inhabit an environment that is highly variable in time and space (Fig 1), but it is also an environment that is dominated by vertical gradients: gradients of physico-chemical properties such as light intensity and quality, temperature, nutrients and hydrostatic pressure, and also of biological properties, such as primary production, standing crop of organisms, predation pressure (particularly from visual predators) and food availability. These gradients are influenced on the broad-scale by water circulation, heat budgets and seasonality and on smaller scales by mesoscale features, fronts, upwelling and finer-scale mixing processes.

Within a population each individual organism is coping with four basic drives: (1) to survive, (2) to feed, (3) to reproduce and (4) to optimize its use of resources. These drives are not necessarily compatible. For example, in response to the need to feed, a planktonic individual will tend to move to shallow depths where there is a greater abundance of food, but in so doing it will experience a greater chance of encountering predators. The level of predation risk an organism accepts will vary

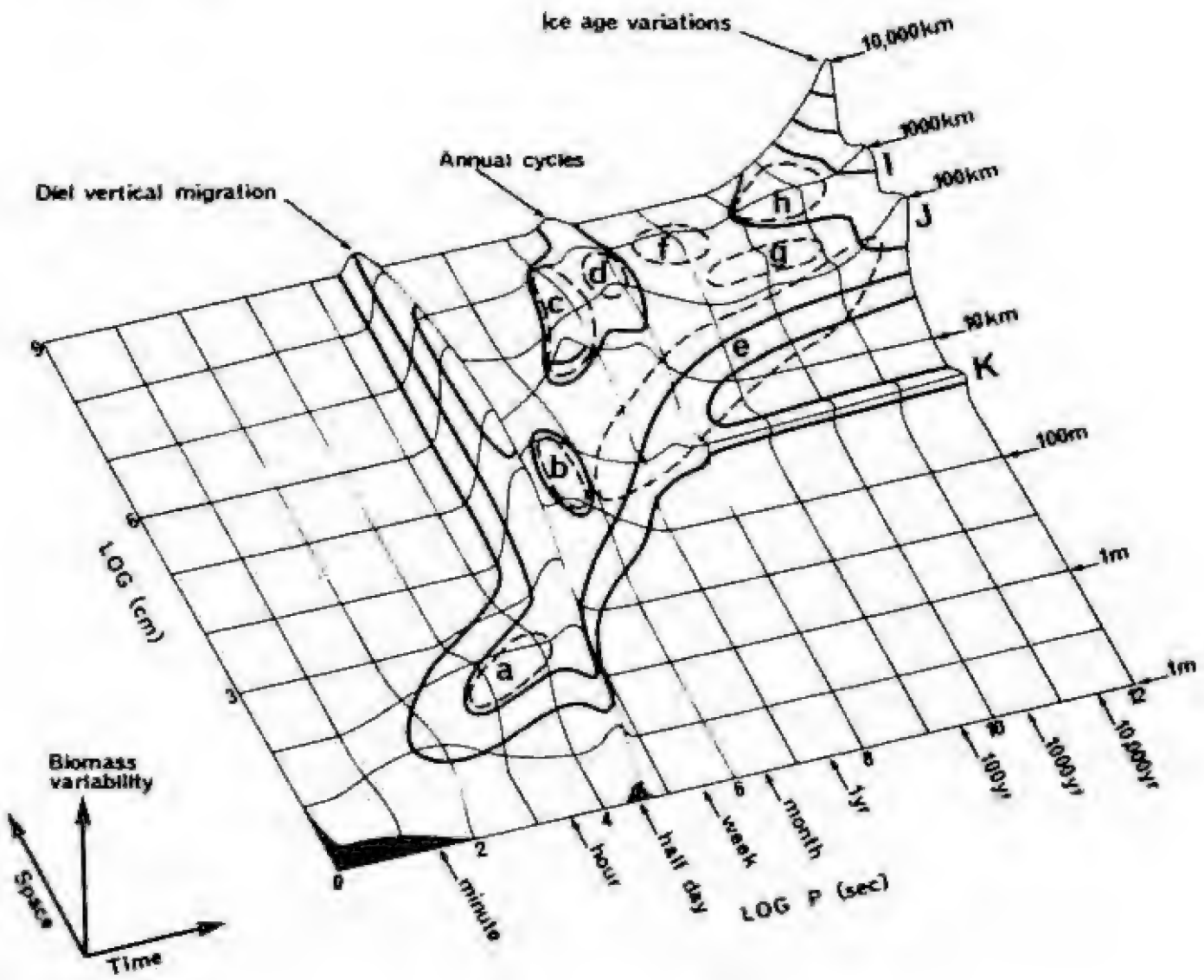

Figure 1

A Stommel diagram showing a visual impression of the possible relationship between time/space variability in zooplankton biomass to major physical processes in the ocean. Maxima in variability are associated with **a**. "micro" patches; **b**. swarms; **c**. upwelling events; **d**. mesoscale eddies and rings;**e**. island effects; **f**. El Nino type events; **g**. small scale oceanic basins; **h**. biogeographical provinces; **i**. length of currents and oceanic fronts; **j**. width of currents; **k**. width of ocean fronts. (After Haury, McGowan and Wiebe 1978).

with its genetical make-up, its stage in the life-cycle, and its nutritional state. For example Huntley and Brooks (1982) have demonstrated that hungry copepods behave quite differently from well fed copepods.

Iwasa (1982) produced a simple model which shows that diel vertical migration is one of the options open to plankton to solve the conflicting needs to feed and to survive in an environment in which there are complementary gradients in food availability and visual predation pressure, particularly if these parameters vary in time (i.e., daily or seasonally). There are alternatives to migration that can be adopted: either reducing susceptibility to predation, reducing demand for food or accepting the high risk. The alternative ploys would not result in any advantage accruing from vertical migration.

The periodicity and intensity of the time/space variability of available food and predation pressure will be major factors in determining the patterns of migratory behavior. Large animals, with a capability of extensive horizontal migrations, will be able to smooth the effects of environmental heterogeneity by horizontal migrations

between widely separated localities. Thus the large whales are able to exploit the massive standing crops that develop at high latitudes during the spring and summer. Then they migrate to lower latitudes during the periods of low productivity where, although they feed less (if at all), the warmer water temperatures allow them to conserve body heat and hence energy. Their migration is also related to reproduction; the calves, which have much lower surface area to volume ratios, lose less heat in the warm tropical waters than at high latitudes.

Planktonic and micronektonic organisms which do not have the capability of performing extensive horizontal migrations (but see Hamner and Hauri 1981) exploit the seasonal variability by seasonal migrations. They feed in the surface layers during periods of high productivity and then return to deep water often entering a state of diapause during periods of low productivity. In some areas of the NE Atlantic, where there is both a spring and an autumn phytoplankton bloom, there may be upward migrations in some species in both seasons (DISCOVERY, unpublished data). In species with annual life cycles, seasonal migrations will be indistinguishable from ontogenetic migrations. However, in those with shorter or longer life cycles, there is a distinction that is important (cf. Longhurst 1976).

At lower latitudes, as the intensity of the pulsing of the seasonal cycle diminishes, so seasonal migration becomes less important. The subtropical convergences, which in most oceans mark the lowest latitude at which winter cooling disrupts the seasonal thermocline and as such marks a sharp break in the seasonality of production, will probably also prove to mark a major change in the intensity or even occurrence of seasonal migration. Seasonal migrations will also be important in areas where seasonal upwelling occurs. In regions where the production cycle is more uniform, life cycles in the surface waters tend to be shorter than the annual cycle, and onotogenetic migrations become more obvious.

Diel vertical migration can be superimposed on both ontogenetic migration and seasonal migration. For example the deep mesopelagic mysid ***Eucopia unguiculata*** is normally considered to be a nonmigrant species, but in the recently published work by Roe (1984a) on the results of time series of hauls at 44°N, 13°W during the spring, this species had moved up to daytime depths of around 450 m and was performing diel migrations to at least 250 m. Later in the year the species occurred below 600 m only.

LIMITS TO DIEL MIGRATIONS

The early report by Waterman, Nunnemacher, Chace and Clarke (1939) described a number of species undertaking extensive vertical migrations from depths of at least 1500 m. Wiebe, Madin, Haury, Harbison and Philbin (1978) interpreted some of their profiles as showing diel migrations of ***Salpa aspersa*** to depths of 2000 m. Even if the data on which these reports were based were correctly interpreted, it now seems likely that most diel migrations are restricted to much shallower depths. Angel, Hargreaves, Kirkpatrick and Domanski (1982) found cyclic variability consistent with a diel migratory cycle only in a single fish species ***Notoscopelus elongatus*** at 1000 m

at 42°N, 17°W. More recent sampling to the southwest of the Azores showed that decapod crustaceans migrated up from around 1200 m and the myctophid ***Ceratoscopelus warmingi*** from 1600 m, in the latter case into the surface 100 m (Badcock, personal communication). At high latitudes, diel migrations are very much reduced in extent, or even absent during the polar summer (Bogorov 1946, Digby 1961). Similarly at equatorial latitudes, diel migrations are very much reduced in extent (e.g., Angel and Fasham 1975, Roger 1974a).

Generally diel migrations are related to the light cycle (see Longhurst 1976 for references); the early hypothesis that organisms follow isolumes has now been modified such that the rate of change in light intensity is thought to provide the major environmental stimulus (Ringelberg 1964, Bary 1967, Kampa 1974, Enright 1977a). Roe (1983) has recently shown that the vertical ranges of many species are so broad that they span at least three orders of magnitude of light intensity; also the observed rates of ascent and descent in a variety of copepod species were much slower than the rate of 120 $m \cdot h^{-1}$ at which the isolumes ascended and descended at near dusk and dawn (Table 1). Enright (1977b) observed comparable rates of 30−90 $m \cdot h^{-1}$ in ***Metridia pacifica***, i.e., 3.5−10 body lengths per second. Endogenous rhythms (Harris 1963, Enright and Hamner 1967) have been observed and may play a role in minimizing the organisms' daytime responses to irrelevant stimuli produced by clouds and solar eclipses (Roger 1974b; Alldredge and King 1980; Bright, Ferrari, Martin and Franceschini 1972). Variations in light intensity at night produced by moonlight will be significant where visual predation is important, and so may be expected to cause adjustments to near-surface vertical distributions (e.g., Roger 1974b). However, it is important throughout to remember that sampling techniques only allow the recognition of migration patterns that are reasonably coherent and synchronized within a population (Pearre 1979). Also, there are numerous reports of cycles that are unsynchronized with light cycles.

Longhurst (1976) in his review of vertical migration listed various hypotheses that have been advanced to explain vertical migration. These are: (1) avoidance of visual predation, (2) horizontal dispersion and transport, and (3) bioenergetic advantages, to which I would add a fourth, breeding migrations.

Throughout it is important to distinguish between the environmental factors controlling migration, the ecological reasons for the migrations and the ecological consequences. In the rest of this paper I wish to explore some of the connotations of each hypothesis and to look for evidence in the literature or my Department's data to support these hypotheses and their ecological implications.

Table 1

Estimated ascent and descent rates in $m \cdot h^{-1}$ by seven copepod species observed at 44°N, 13°W during four sets of 48 h observations in April 1974 (Roe 1984c).

	Upward		Downward	
	Mean	Range	Mean	Range
Gaetanus minor	43.0	32–57	41.7	28–65
Metridia lucens	81.3	47–130	61.9	36–99
Pleuromamma robusta	84.3	58–117	86.2	57–108
Chirundina streetsi	85.8	63–119	96.8	66–148
Euchirella curticauda	107.5	71–168	100.2	69–148
Undeuchaeta major	122.2	86–168	100.2	69–148
Undeuchaeta plumosa	122.2	86–168	121.8	99–143

THE AVOIDANCE OF VISUAL PREDATION

One of the earliest theories put forward to explain diel migration postulated that vertical movement afforded escape from predation (Russell 1927). This idea came back into vogue with some of the elegant work on the influence of predation on freshwater communities and on cyclomorphosis (see review by Zaret 1980 and Stich and Lampert 1981). The generally tight relationship between migration cycles and light cycles is consistent with this hypothesis. If the theory be valid, then minimum daytime depths should relate to where the organism ceases to present a perceptible visual cue. Because visual acuity declines with diminishing light intensity, this should create a depth-size relationship with planktonic communities and hence provide possible cause for ontogenetic migration in which progressively older and larger stages occur progressively deeper by day. In micronekton the depth zonation should be related to camouflage systems; similarly nonmigrants should be adapted to reduce their visibility either by being small or transparent. Another effect might be for herbivores to perform reverse migrations where the primary carnivores vacate the surface layers to avoid predation by secondary carnivores. Similarly, even if the predation is unlikely to be visual (e.g., as for highly transparent organisms such as salps), any cyclic feeding pattern of migration by the carnivores may result in an advantage to the prey undertaking vertical migrations. These are all phenomena which have been reported in the literature.

Angel (1979) analyzed the size spectra of the ostracod populations in the vicinity of Bermuda and found that the maximum size of individuals in the population increased in a stepwise manner with depth (Fig 2). Each step corresponded to a change in the classical depth zones, i.e., the size range increased across the seasonal thermocline, between the epipelagic and shallow mesopelagic (at ca. 300 m), between the shallow and deep mesopelagic (at ca. 500 m), and at ca. 700 m. Each one of these steps coincided with a change in the morphology of the daytime nekton

community—for example 300 m was the ceiling of the distribution of silvery-sided fishes with well-developed ventral photophores (e.g., myctophids and hatchetfishes) and at 500 m there was a change between decapod species that were half red and half transparent to those that were totally red (cf. Foxton 1972).

There was an ontogenetic daytime ascent of the larval stages in some of the ostracods, as in ***Conchoecia imbricata*** (Fig 3), whereas at night the depth ranges of all the oldest juvenile instars and the adults became almost identical as a result of vertical migration. Similarly the size spectra of the total ostracod population became similar at all sampling depths from the surface to 700 m. This lower depth was the depth limit of appreciable migration by the planktonic ostracods but not of the micronektonic species (IOS, unpublished data; Donaldson 1975). The lowest depth from which vertical migration would be expected to occur would be the maximum depth at which the individual organisms are capable of detecting the down-welling daylight. This has been placed at around 1000−1200 m, and in many areas in the NE Atlantic this does indeed seem to be the lower limit of vertical movements (e.g., Angel et al. 1982; IOS, unpublished data). Some but not all of the reports of deeper diel migrations are suspect. For example, Waterman et al. (1939) had only four sets of hauls and a factor of two covered their maximum change in abundance, which Angel et al. (1982) concluded was the minimum sampling variability to be expected in repeated deep tows. Wiebe et al. (1978) had good data for the diel migration of the salp ***Salpa aspera*** to below 800 m, but only circumstantial evidence of its migration between 2000 m and the surface waters. Baird, Wilson and Milliken (1973) showed the deep penetration of the codlet ***Bregmaceros nectabanus*** into the anoxic water of the Cariaco Trench. To the southwest of the Azores we have recently found a myctophid ***Ceratoscopelus warmingi*** which migrated from 1600 m up into the surface 100 m at night (Badcock, personal communication); the migrations of other micronektonic species were restricted to above 1200 m.

Comparative studies of vertical migrations from broad-ranging zoogeographical areas would be useful in showing whether shifts in predation patterns result in changes in migratory behavior. Such shifts might be associated with the immigration/emigration of key predators or might occur as a result of the normal seasonal succession. In freshwaters it has been shown that ***invertebrate*** predation tends to be nonvisual (e.g., Kerfoot 1977, Zaret 1980) and tends to favor the development of large herbivores that do not perform diel migrations and that are "fitted" with anti-handling devices such as long spines. At abyssal depths there is a trend toward gigantism in invertebrates (Mauchline 1972) which is often associated with buoyancy mechanisms that require a large body water content; possibly predation patterns play a role in this phenomenon (Angel 1983a).

The predation avoidance theory would argue that in the absence of any other advantages, the top predators would not need to migrate although their presence might well induce migration by their prey; if the migratory prey were also carnivores, their movements might in turn induce an aberrant migration pattern in the food organisms. An example of the complex interactions that can occur has recently been described from a temperate fjord off Washington on the west coast of America by Ohman, Frost

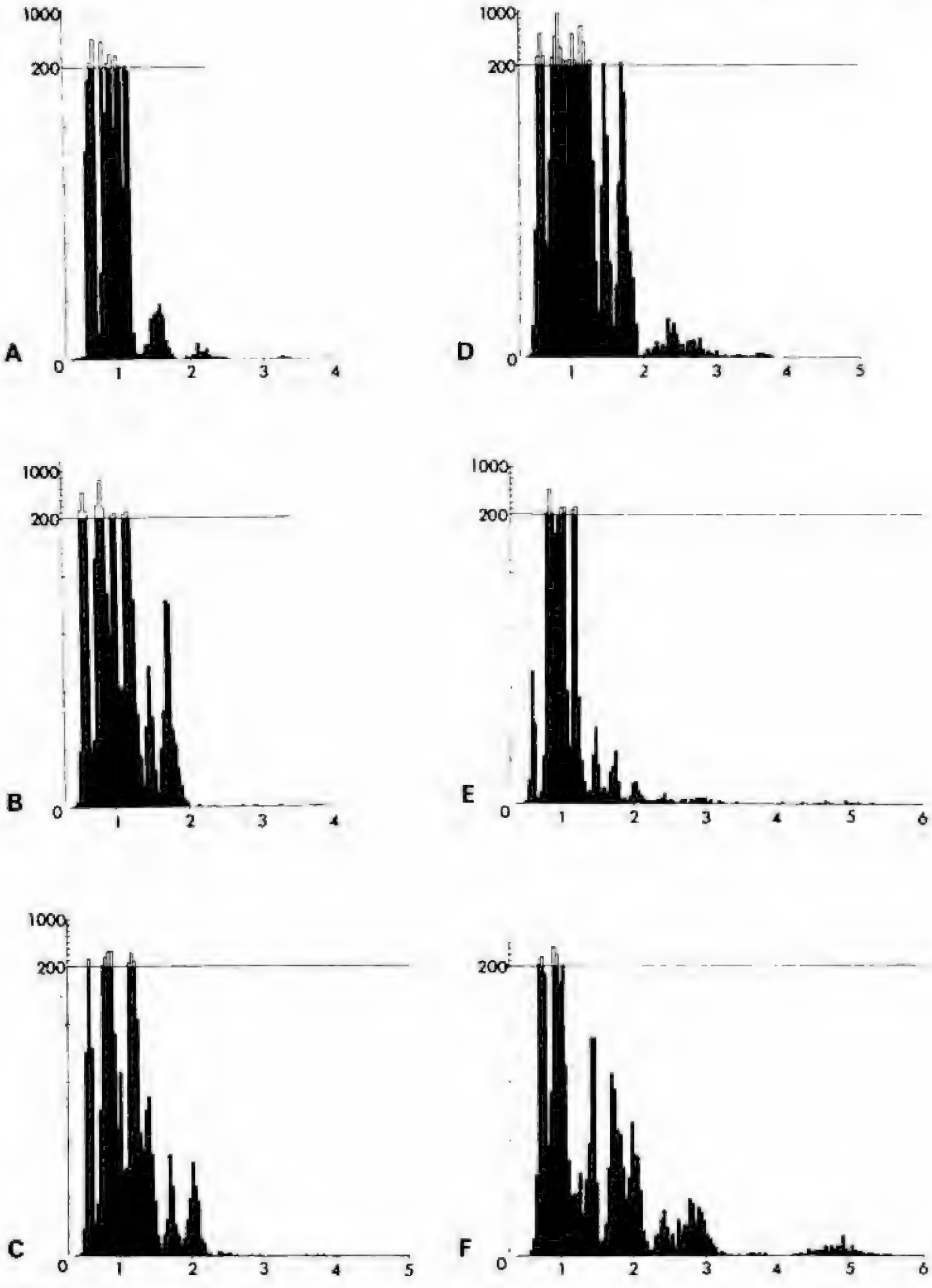

Figure 2

Population size spectra of planktonic ostracod communities sampled at 32°N, 64°W near Bermuda in March 1973. Carapace lengths are in millimeters and the sample size has been scaled to make the volume of water filtered equivalent in all samples. Note that the vertical scale changes at numbers > 200. A. 100–50 m day; B. 100–50 m night; C. 300–200 m day; D. 300–200 m night; E. 400–500 m day; F. 600–700 m day. Note how the spectra extend with depth and at night as the result of diel migration (from Angel 1979).

and Cohen (1982). There the main herbivore is ***Pseudocalanus*** sp. which in August develops a reverse migration, swimming up by day and down at night. Its main predators, a chaetognath ***Sagitta elegans*** and a copepod ***Euchaeta elongata***, both of which are nonvisual feeders, become abundant in August. The secondary carnivores, planktivorous fish (e.g., juvenile chum salmon and sticklebacks), feed visually, and this, as might be expected, induces the two primary carnivores to perform normal migrations. ***Pseudocalanus*** adopts a reverse migration in August which the authors postulate minimizes the frequency of encounters with the primary carnivores and so results in enhanced survival. In the absence of predation, ***Pseudocalanus*** is nonmigratory and remains in the surface layers. As a nonmigrator, ***Pseudocalanus*** has a higher rate of increase than if it was migratory; this is because any increase in its fecundity associated with the cooler temperatures experienced by the migrators at their daytime depths is more than offset by a decline in survival. Ohman et al. (1982) estimate that a 16% reduction in mortality through predation is needed for migration to become the better option.

Perhaps one of the major doubts arises from the seas with relatively little deep thermal structure such as the Mediterranean and the Red Sea. These seas do not appear to have the same vertical zonation of organisms within the water column and lack a typical bathypelagic fauna (e.g., Weikert 1980). The usual explanation is that the shallow depths of the entrances prevent the immigration of bathypelagic species from outside (e.g., Furnestin 1979). However, this does not explain why an endemic bathypelagic fauna has not evolved. The lack of classical vertical structuring of the communities may result in some of the aberrant migration patterns described from the Mediterranean (e.g., Huré and Scotto di Carlo 1974).

LIFE-CYCLE MIGRATIONS

Successful spawning involves two phases, mating (i.e., sperm transfer) and egg-laying. In many species the phases are simultaneous with fertilization occurring as the eggs are spawned. However, in some species that store sperm and in all of those that brood their young, the two phases may be widely separated in both time and space. Mating requires the successful location of a mate and for small organisms in a vast three dimensional environment this must pose quite a problem. A solution might be long-distance communication as by the release of sexual attractant pheromones; this strategy might be particularly effective if the swarming or release of pheromone by one sex occurs (e.g., Hamner and Carleton 1979) within a layer through which the other sex oscillates. Reduction of the mating search from 3 to 2 dimensions may be the function of mono-sex swarms at the surface, as observed in the males of the ostracod ***Conchoecia spinirostris*** (Moguilevsky and Angel 1975). Female swarms have been reported in some shallow water copepods (Ueda, Kuwahara, Tanaka and Azeta 1983). In another ostracod ***Halocypria globosa***, males occur only at deep mesopelagic depths (Fig 4) to which the females presumably swim to locate them (Angel 1979). Sexual dimorphism in both vertical distribution ranges and vertical migration is quite a common feature in a whole range of species (e.g.,

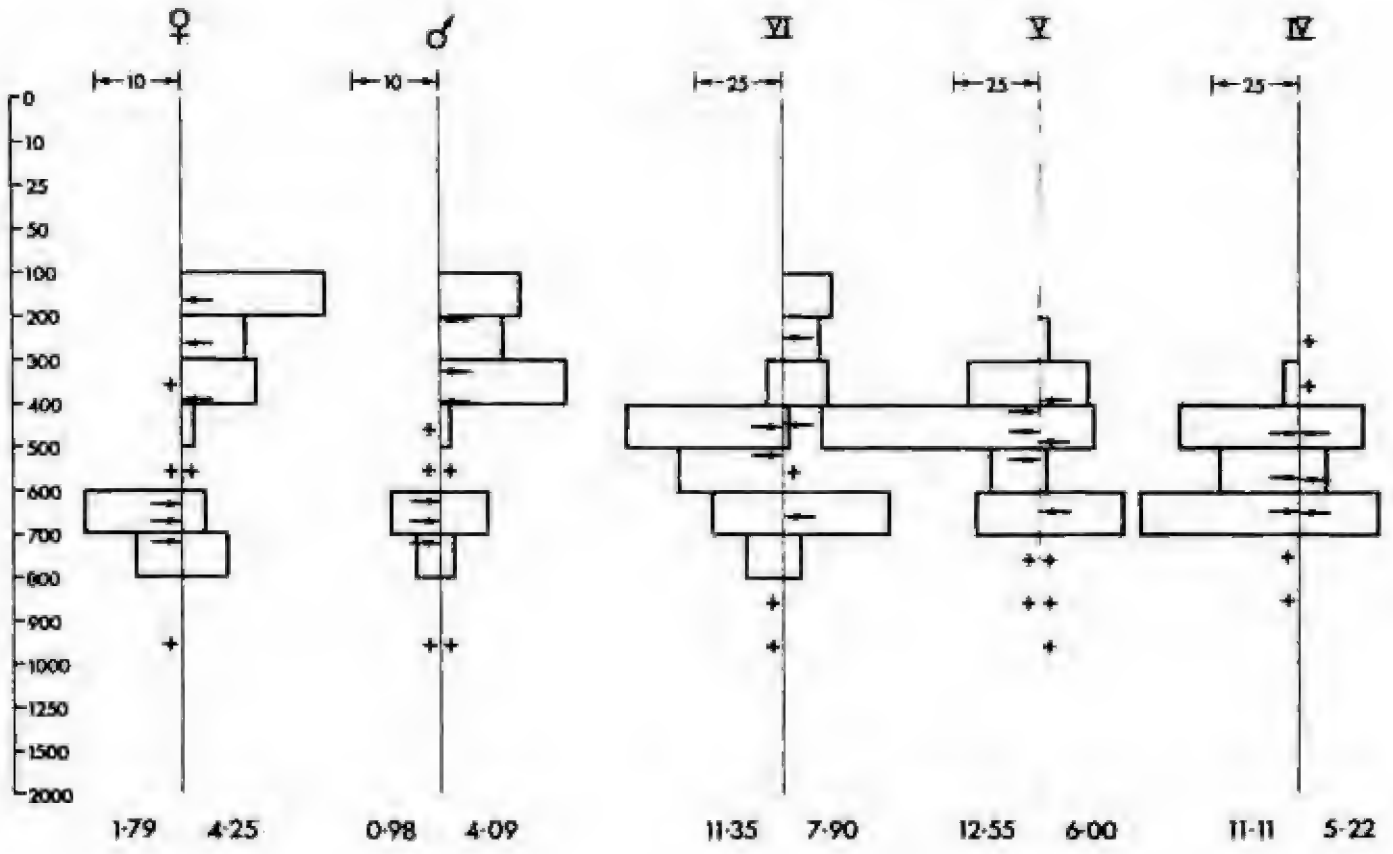

Figure 3

Profiles of the vertical distribution of the planktonic ostracod *Conchoecia imbricata* at Ocean Acre 32°N, 64°W near Bermuda in March 1973, showing daytime (left) and nighttime (right) distributions of females, males and the three oldest larval instars. Figures at the bottom of each profile indicate the number of each stage per m^2 of sea surface to the maximum depth sampled (2000 m). Arrows indicate the quartile depths, and abundances are given in number per 1000 m^3 water filtered. Note the ontogenetic development of diel vertical migration (from Angel 1979). + indicates presence in abundance of < 1 per 1000 m^3 filtered.

Furuhashi 1976, Matsuo and Marumo 1982, Hayward 1981).

In the ostracods that store sperm, the eggs are generally neutrally buoyant (Angel 1972) and may be released at a depth totally different from that at which mating occurred. Those euphausiids which spawn directly into the water have eggs that are heavier than water; euphausiids also store sperm, so mating and egg-laying do not coincide. Euphausiid egg sinking rates of $5-7.5\ m \cdot h^{-1}$ have been observed for ***Thysanoessa raschi*** and ***Meganyctiphanes norvegica*** (Mauchline and Fisher 1969). Hatching takes several days, so it has been speculated that the eggs of the Antarctic krill ***Euphausia superba*** may sink to depths of 1500 m prior to hatching (Marr 1962). The newly hatched naupliar larvae are nonfeeding and start a developmental ascent (see Roe, James and Thurston 1984, for data on other species). They arrive in the surface layers as they molt from the metanaupliar to the first feeding stage, the calyptopes. As the calyptopes develop they start to display a diel migratory behavior. Hence the deep water, where particulate feeders are relatively infrequent, is used as a refuge for the nonfeeding stages. The feeding stages then occupy the food-rich surface layers, and develop diel migratory behavior as they grow and become more vulnerable to predation. In general there is a total lack of data on the depth of egg-laying in the vast majority of planktonic species.

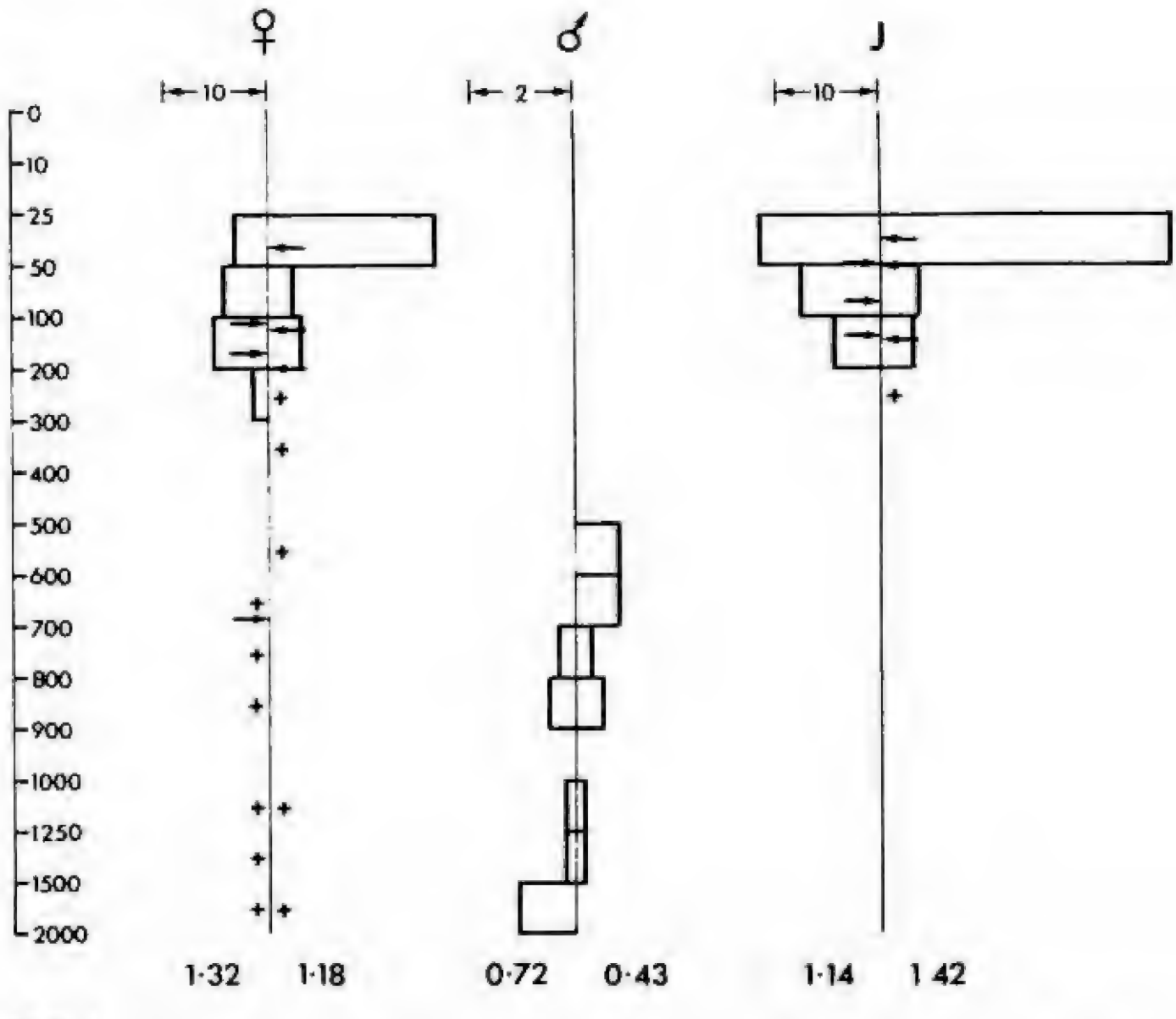

Figure 4

Profiles of the vertical distribution of the planktonic ostracod ***Halocypria globosa*** at 30°N, 23°W in April 1972 showing daytime distributions to the left and nighttime to the right of males, females and all larval instars. Figures at the bottom of each profile indicate the number of each group per m^2 of sea surface. Arrows indicate the quartile depths and abundances are given in numbers per 1000 m^3 water filtered. Note the substantial differences in the profiles for males and females (from Angel 1979). + indicates pressure in abundance of < 1 per 1000 m^3 filtered.

If in the oceans, as in freshwater environments, a large size ensures better survival in the presence of invertebrate predation pressure, then rapid growth will improve the chance of larval survival. However, as larval size increases, and vulnerability to visual predation increases, so diel migration behavior may progressively develop. The type and pattern of predation will influence not only migration but also the life-history "strategy" adopted by a species.

Another phase of the life cycle in crustacean plankton when vulnerability to predation may be increased will be at the time of molting. Once again, there appears to be no information published on whether molting is accompanied either by a change in vertical distribution or by a modification in diel migration.

McLaren (1963) suggested that vertical migration provides a demographic advantage to the migrant. The time spent at cooler depths results in larger, more viable eggs being produced which hatch into larvae with greater potential survivorship. This opens into the field of life history strategy which is outside the scope of this paper. It is relevant to record, however, that Orcutt and Porter (1983) have shown

experimentally that ***Daphnia*** gain no added fitness in an oscillating temperature regime. In this case maximum fitness was achieved by remaining in the warmest surface waters.

HORIZONTAL DISPERSION AND MIGRATION

In a patchy environment vertical movements exploiting the progressive increase in relative shear with depth may be an effective way of either locating favorable patches or escaping from unfavorable ones. The idea originated from Hardy and Gunther (1935) who were trying to explain why it was rare to find patches of abundant zooplankton which coincided with rich patches of phytoplankton. They argued, based on their experience of toxic red-tides, that dense phytoplankton blooms excluded zooplankton by toxic excretions. Now the general consensus is to reverse the interpretation since blooms of phytoplankton can only develop where (a) the nutrient supply is adequate, (b) the surface layers of water column are relatively stable vertically, and (c) the grazing pressure of the herbivorous plankton is not so intense that it limits the rate at which the phytoplankton population grows.

It would seem likely, but it is still controversial, that many filter-feeding herbivores have feeding thresholds governed by the food concentration at which energy expended on feeding exceeds the metabolic gain. Thus, rather than avoiding phytoplankton patches, the zooplankton may use vertical oscillations as a means of horizontal movement to locate phytoplankton patches. Even in microzooplankton such as Foraminifera and Radiolaria, it has been postulated that an important function of the heavy skeleton is to provide these nonmotile organisms with a mechanism whereby they can sink rapidly and so perform vertical migrations (Marszalek 1982).

There is evidence that at least some plankton is capable of quite extensive horizontal migrations, e.g., the scyphozoan ***Mastigias*** (Hamner and Hauri 1981) and krill ***Euphasia superba*** (Kanda, Takagi and Seki 1982). Complex migrations of ***Mastigias*** have been observed in a marine lake in Palau; individual animals may move horizontally as much as a kilometer a day and also undergo a vertical migration down to a shallow chemocline at night. Such observations warn us against simplistically assuming that planktonic organisms neither undertake, nor are capable of undertaking, horizontal migrations because they have rarely been observed to do so. It would be a useful modeling exercise to investigate the relative advantages of horizontal versus vertical migration for locating patches of food of different size and frequency, so proper field observations can be designed.

Isaacs, Tont and Wicks (1974) investigated the vertical movement of deep scattering layers (DSL's) and showed that the range of migration tends to be reduced in areas of higher productivity probably because of the greater absorption of light which resulted from the higher standing crop. As the relative shear between the surface layers and deep water increases with depth, this would result statistically in the aggregation of the organisms responsible for the DSL within the zone of elevated production. Further evidence for this sort of effect came out of some recent investigations into the biological processes at a front between Western Atlantic Water

(i.e., typical 18°C Sargasso Sea water) and Eastern Atlantic Water to the southwest of the Azores. Observed vertical profiles in the two water masses and in the front showed that the integrated standing crop of micronekton was higher in the front and the range and pattern of vertical migration changed quite substantially. The integrated standing crop of phytoplankton as estimated by chlorophyll *a* concentrations was scarcely higher in the front than elsewhere and insufficient to make a noticeable difference in the observed light profiles. There was no correlation between the migration ranges and the isotherms. Thus the next factor to consider is the distribution of availability of food.

If seeking food is an important function of vertical migration, then variations in the quantity and quality of available food might be expected to modify migratory behavior. On the basis of the Isaacs et al. (1974) model, as food availability declines, so the range of vertical excursions might be expected to increase. However, the only reliable experimental evidence comes from the study by Huntley and Brooks (1982) of *Calanus pacificus* in a plankton tower during which shortage of food inhibited diel vertical migration by copepodites which remained at shallow depths throughout the 24 h cycle.

In this case, one interpretation could be that by adopting a nonmigratory behavior and remaining at a shallow depth, the population of *Calanus* was following the option which gave the maximum probability of survival within the normal spectrum of space/time variability of its environment. For another species from a different ecosystem, or even another race of the same *Calanus* species, a totally different response to starvation may occur. This whole question of the influence of nutritional state on migratory behavior needs investigation in a range of species, both experimentally and by field observations.

The exploitation of differential current shears between shallow and deep waters is an important mechanism whereby planktonic organisms can avoid dispersion out of a hydrographic system. The time scales of the physical processes in the system will influence the type of migration that is important. Thus in estuaries, diel or totally synchronized migrations between the deep inflow and the shallow outflow maintain planktonic organisms within the system (Lance 1960, Grindley 1964, Bosch and Taylor 1973). Within larger-scale systems, such as the Somali Current gyre, *Calanoides carinatus* has a life-cycle tuned to the physical characteristics of the system which, through a combination of diapause and ontogenetic migrations, results in the rich upwelled waters in the upwelling zone being seeded with vast numbers of the copepod (Smith 1982). In such dynamic regions, the distribution patterns of the organisms are often much tighter than would be expected if they were merely passive markers. On an even larger scale the seasonal migrations of *Calanus finmarchicus* have been postulated as the mechanism whereby the zoogeographical distribution of the species is maintained in the N Atlantic (Jashnov 1970). Kelly, Sulkin and Van Heukelem (1982) showed a similar tuning between life cycle and distribution in *Geryon quiquedens*.

BIOENERGETIC ADVANTAGES

McLaren (1963) postulated that by migrating between two temperature regimes, migrants would be more efficient in their use of energy since at lower temperatures metabolism is less demanding of energy so more is available for growth. Furthermore, because at low temperatures fewer large eggs tend to be produced, the offspring of migrants would grow faster and be larger to handle and so demographically on balance, would have a better chance of survival than the offspring of nonmigrants. McAllister (1971) and Kerfoot (1970) suggested that there is also an advantage to be gained from pulsed grazing, particularly when the growth cycle of phytoplankton is diel with cell division occurring just before dusk. Phytoplankton cells have the daylight period in which to photosynthesize and feeding becomes more efficient when the cell concentration increases sharply near dusk. Enright (1977a), recognizing that this theory as stated required a measure of altruism by the species involved (e.g., Miller, Pearcy and Schonzeit 1972; McLaren 1974), developed a model that illustrated that there could be bioenergetic gain to the individual animal if three assumptions were fulfilled. These were: (1) the algal biomass can increase appreciably between dawn and dusk, (2) the metabolic needs of the animals are reduced in cooler deeper, water and (3) the grazing rate of the herbivores after a period of nonfeeding is initially higher than the steady state but declines quite quickly. He showed that one prediction of the model would be that grazers could gain a substantial advantage in migrating up 2−3 h before sunset. Enright and Honegger (1977) investigated the timing of migrations in three 3-day series of samples and obtained a measure of confirmation. Off California in early summer the copepod ***Calanus helgolandicus*** migrated up after sunset, but in late spring both adults and copepodites arrived 1−2 hours prior to sunset. In midspring the adults arrived at sunset but the copepodites arrived early, implying an ontogenetic change in the cost-benefit ratio of greater nutrient gain vs. increased exposure to predation.

Perhaps one assumption by Enright (1977a) that is suspect is that the metabolic needs of animals are reduced at depth. Teal (1971) showed that increasing hydrostatic pressure can stimulate metabolism and so negate the influence of low temperature, although Belman (1978) showed that increased hydrostatic pressure had no effect on the oxygen consumption of the squid ***Histioteuthis heteropsis***. In some regions, such as the NE Atlantic at 44°N, 13°W, the temperature differential between day and night depths of mesopelagic migrants moving 300−400 m may be less than 2°C (e.g., Roe 1984b). Childress, Taylor, Caillet and Prince (1980) have shown that the metabolism of vertically-migrating mesopelagic fish is very different than that of nonmigrants either from the epipelagic or from the mesopelagic or bathypelagic. The mesopelagic migrants give higher priority to energy storage than growth. As sexual maturity is attained and the growth rate declines, as in the case of the myctophid ***Benthosema glaciale***, there is a switch from a daily cyclic pattern of feeding by juveniles to continuous feeding in adults (Roe and Badcock 1984). Although in developing his model, Enright considered herbivores only, his argument could be just as valid for a carnivore if herbivores with full guts are more nutritious than ones with empty guts.

Table 2

Integrated standing stock in the top 1200 m of the water column at five central North Atlantic stations situated close to an oceanic front to the SW of the Azores of nekton (based on total RMT8 samples) and plankton (based on RMT1 samples less the larger organisms also taken by the RMT8) expressed as cc displacement volume per m^2, and the diel fluxes of biomass into and out of the surface 200 m and 500 m. All the positions were located within 300 nm of each other. WAW position was in western Atlantic water (18°C water); WAWF was in western Atlantic water but inside a meander in the Front; Front was situated actually within the 20 km wide frontal zone and the sampling was carried out parallel to the front; EAW was in Eastern Atlantic Water typical of a region extending eastwards to the Iberian coast and northwards to about 40°N; Eddy was situated in a cold core eddy of EAW which was spawned from a meander in the front two months prior to the sampling. Day data, which are subject to error because of avoidance, have been standardized to give equivalent integrated estimates to the nighttime estimates at each position assuming the degree of avoidance does not change with depth. Plankton data in parentheses for WAWF are based on total RMT1 samples, without subtracting the nektonic content of the catches.

	WAW	WAWF	Front	EAW	Eddy
Integrated standing stock					
Plankton	9.3	(23.8)	24.3	16.3	14.2
Percent reduction by day	2	28	35	18	−7
Nekton	5.4	7.4	14.4	9.1	8.7
Percent reduction by day	32.5	19.5	37.5	19	0
Flux per m^2 into the surface 200 m at night					
Plankton flux	1.2	(1.5)	3.4	3.0	3.0
Percent standing crop	12.9	6.3	14.0	18.4	12.1
Nekton flux	0.9	1.6	3.2	1.6	1.2
Percent standing crop	16.6	21.6	22.2	17.6	13.8
P:N	1:0.75	(1:1.06)	1:0.94	1:0.53	1:0.40
Flux per m^2 into the surface 500 m at night					
Plankton flux	0.7	(1.6)	0	1.7	0.9
Percent standing crop	7.5	6.7	0	10.4	6.3
Nekton flux	1.0	2.1	3.1	1.8	1.6
Percent standing crop	18.5	28.4	21.5	19.8	18.4
P:N	1:1.43	(1:1.33)	1:0	1:1.06	1:1.78

However, observations on the time of migrations rarely support the Enright model (e.g., Roe 1974; Roe, Angel, Badcock, Domanski, James, Pugh and Thurston 1984, and the subsequent papers), but there is a considerable lack of suitable observational data.

The most persuasive argument against the importance of the energetic bonus of vertical migration comes from the study by Torres and Childress (1983) on ***Euphausia pacifica***. They showed that in the California Current region, the cost of vertical migration cancels any energetic gain from time spent at lower temperatures. They point out that because their measurements imply that active swimming is substantially more costly, particularly at higher temperatures, in water columns where the temperature gradient is small, more energy is likely to be expended by migrating than by staying in the warmer surface waters. However, where the temperature gradient is sharp, such as in the central Pacific where the temperature differential between the surface and 500 m is 16°C, a substantial benefit would ensue. Hence the energy bonus of vertical migration is more likely to be important at low latitudes.

VARIATIONS IN VERTICAL MIGRATIONS RELATED TO PHYSICAL VARIABILITY

Despite the vast literature on diel migration, there has been surprisingly little effort to quantify the effects of such movements. Longhurst (1976) attempted some order of magnitude estimates, and using a plankton standing crop estimate of 25 $g \cdot m^{-2}$ in the surface 100 m, he assumed a 10% increase from depths > 250 m, which gave a translocation of 2.5 $tons \cdot km^{-2} \cdot d^{-1}$.

During the summer of 1982 the DISCOVERY occupied five stations all within a relatively small area to the southwest of the Azores. The stations were to either side or within a major oceanic front which formed the eastern boundary of the main mass of 18°C Sargasso Sea water (Gould 1985) and also probably represented one of the return flows of the Gulf Stream. The specific composition changes very little across the front (Pugh 1975; Angel 1979; James, personal communication). Yet the depths of the biomass quartiles for both nekton and plankton based on catches to 1400 m showed quite substantial variation relative to the front. Estimating the vertical flux of biomass is difficult because daytime catches particularly of euphausiids are lower than nighttime catches. In Table 2 the nighttime standing crops, which have been estimated by integrating the observed concentrations of catch displacement volumes over the upper 1200 m of the water column, are listed together with the percentage decrease in the daytime estimate. If it is assumed that avoidance is constant with depth, and each day and night profile is expressed in terms of the percentage of the total water column standing crop occurring within each depth station, the percentage increase in standing crop in the top 200 m and 500 m can be estimated. Because the degree of avoidance probably varies with depth, these estimates are likely to be excessive. For example, in most profiles, integrated standing crops for plankton below 500 m are almost identical at all stations by day and by night. The percentage of the standing crop moving up into the surface 200 m ranges from 6.2−22.2 for plankton and 9.1−32.0

for nekton; the values for 500 m are 5.3−15.3 and 9.8−31.4 respectively. The Western Atlantic Water estimates of the fluxes are lower by a factor of at least three for plankton, but are comparable for nekton. The nekton flux in the front is higher by around a factor of two. In the eddy the plankton flux is intermediate between the front and Eastern Atlantic Water, but for nekton it is lower than both. These figures are open to considerable doubt, so they are offered here as tentative evidence that major variations in migration patterns may occur in relation to hydrographic features.

Data for individual groups of micronekton are presented in Table 3. Displacement volume data for the front station are unfortunately not available. The day/night disparity, which probably results from avoidance, is most marked for euphausiids; otherwise only at one station each for fish and decapods does the disparity substantially exceed 90%. The disparities based on numerical abundance are very similar. Wiebe and Boyd (1978) in their study of ***Nematoscelis megalops*** in a Gulf Stream ring concluded that avoidance was not a depth-related phenomenon in this species, and so the shapes of their profiles were not seriously affected. Although this conclusion is unlikely to be true for mixed species populations, in order to get a first order estimate of the fluxes, the day data for each individual profile have been standardized to give the same total water column biomass as observed at night. In groups in which avoidance may not prove to be a significant source of error, the variability between profiles seems to be 10−11%.

Three groups, decapods, fish and euphausiids, provide 35−77% of the diel flux in and out of the surface 200 m and 50−110% of the diel flux above 500 m. (The value greater than 100% at the eddy station is mostly offset by the reverse migration of chaetognaths.) These fluxes are subject to considerable variability between both taxonomic groups and different hydrographic regimes. Variations in herbivores and carnivores will have an important influence on grazing and predation pressures, on the flow of material through the pelagic ecosystem, and on the recycling of nutrients within the surface 200 m.

IMPLICATIONS OF DIEL MIGRATION

Genetic

David (1961) suggested that one effect of diel vertical migration would be to increase the gene flow through oceanic populations. The differential current shear between shallow and deep layers will result in the greater rate of dispersion in species in which the migrations were not precisely synchronized or in which there were ontogenetic or sexual differences in migratory behavior. However, in species which are adapted to stay within a current or estuarine system, the migration will equally well function as an isolating mechanism; any genetic variants whose behavior becomes less well tuned to the physical system will tend to be lost from the system.

Table 3

Biomass flux (cc DV·m^{-2}) of four of the dominant micronekton groups in the RMT8 samples at four stations in the central North Atlantic. Day data were standardized to give the equivalent total water column (to 1200 m) standing crops as night data.

	WAW	WAWF	EAW	Eddy
Into Surface 200m				
Chaetognaths	−0.02	−0.03	−0.03	−0.01
Decapods	0.03	0.22	0.20	0.16
Euphausiids	0.16	0.11	0.25	0.24
Fish	0.10	0.34	0.67	0.40
Into Surface 500 m				
Chaetognaths	−0.08	−0.04	−0.01	−0.14
Decapods	0.21	0.52	0.43	0.42
Euphausiids	0.19	0.14	0.30	0.28
Fish	0.39	0.60	0.93	1.10
$D \times \frac{100}{N}$ for Total Biomass Estimates				
Chaetognaths	111	92	101	92
Decapods	108	98	74	97
Euphausiids	58	79	101	72
Fish	77	94	98	89

Patterns of Grazing and Predation

Roe (1984a) and Roe and Badcock (1984) have summarized part of a vast array of feeding data and show how the chronology of feeding varies considerably between different migrants and nonmigrants. Even within an individual species, such as a myctophid fish, feeding chronology changes during development. The diets of species that feed continuously during their migration cycle change, partly because of changes in prey availability and partly because of selectivity changes. Roe's (1984a) data for the decapod ***Systellaspis debilis*** are shown in Figure 5, and illustrate the changes in diet that occur between day, when the animal is abundant at 450 m, and night when it was abundant at 100 m. Roe (1984a) was also able to show that the two species of ***Acanthephyra*** never directly competed in time or space. Thus migration probably leads towards greater resource partitioning in many cases. It would be interesting to contrast the migratory behavior and feeding patterns of similar pairs of species between regions where pairs either co-occur or do not, in order to look for evidence of

character displacement. Character displacement (e.g., Angel 1982) is evidence of interspecific competition between closely related species, and may be limited seasonally or to certain parts of the life-cycle.

The way in which variations in predation pressure and possibly competition may feedback into the function and structure of pelagic ecosystems is illustrated by the work of Ohman, Frost and Cohen (1983) already discussed. However, considerably more data are required on feeding chronology and physiology together with selectivity in diet of midwater organisms. The same limitation is evident in the way in which vertical migration influences the flow of energy and material through pelagic ecosystems.

Energy Flow through Ecosystems

Vinogradov (1970) postulated the migration ladder hypothesis to explain how sufficient organic material reaches deep-living communities. Since then, extensive sediment trap data have suggested that 10% of surface production sinks below 400 m and 1−3% reaches the sea bed at depths of 5000 m (e.g., Honjo, Manganini and Cole 1982). However, Angel (1983b) has argued that the sediment traps are (1) unlikely to catch the large, rarer fecal material produced by nektonic organisms and (2) will totally miss material which moves down within the guts of migrants. Actual migration rates of micronekton (see Table 4) are as fast or faster than the sinking rates of large fecal pellets—some salp fecal pellets sink at 1000−2000 $m \cdot d^{-1}$ which is equivalent to 40−80 $m \cdot h^{1}$ (see Angel 1983b). The deeper a pellet is released, the lower is its likelihood of either being intercepted in midwater (because of the progressive decline in the standing crop of deep-living detritivores with depth, e.g., Angel and Baker 1983) or of being substantially degraded by micro-organisms (because of the cold water temperatures). So, if the gut retention times of extensive migrants is such that they void their guts at daytime depths before beginning their dusk ascent (which could reduce the organisms' density and so make the ascent less expensive in energy), the migrants could make a substantial contribution to the flow of material into deepwater. Hence the flow of labile organic material could be much faster than is generally believed at present, and be much more directly linked to surface productivity in regions and at times of year when migration ranges are extensive.

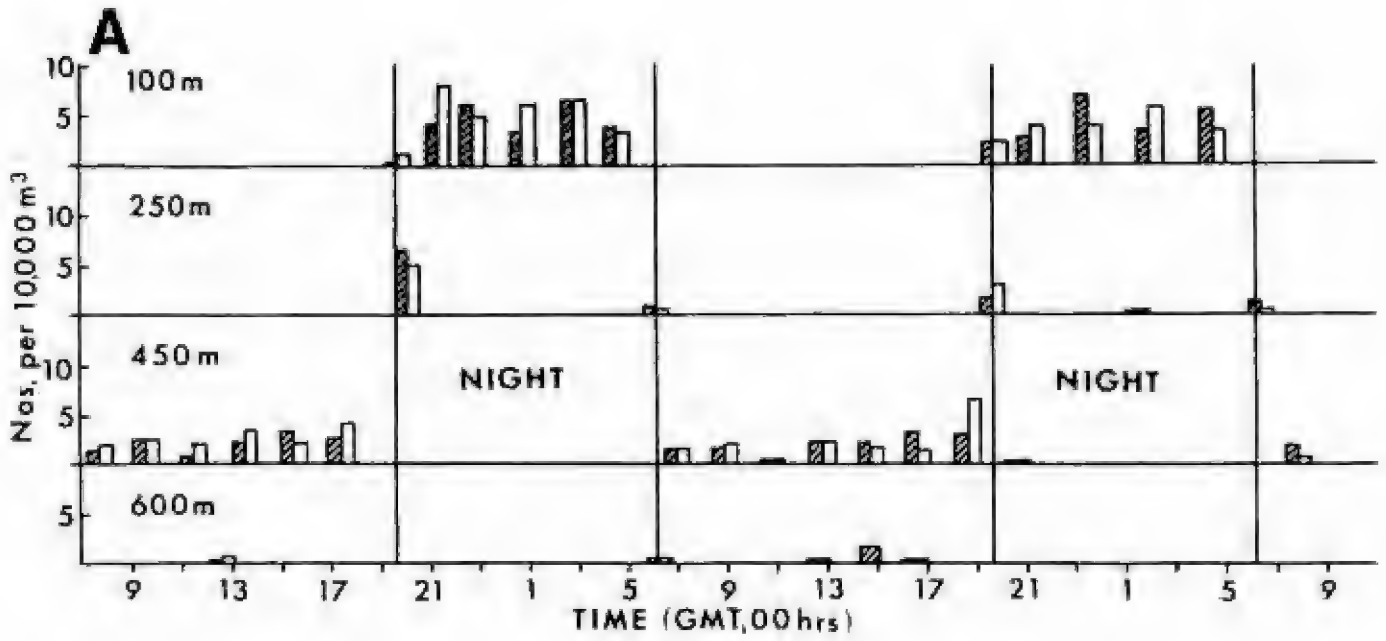

Figure 5

Diel vertical migration in the micronektonic decapod crustacean, ***Systellaspis debilis*** at 44°N, 13°W during April, 1974. A. Abundance of males (shaded) and females over four 48-h periods at four depth horizons in 1-h horizontal tows. B. The mean number of prey per animal (i) the percentage occurrence of each food type (ii) 1. fish, 2. decapods, 3. euphausiids, 4. copepods, 5. chaetognaths, 6. crustacean setae and 7. green detritus in the stomachs of adult *S. debilis*. Sample size (N) and the number of stomachs containing food are shown for each data set. In addition to changes in the proportion of each group, specific composition of copepods and euphausiids changed significantly with depth (from Roe 1984c).

Table 4

Examples of estimates of mean population migration rates ($m \cdot h^{-1}$) from 1. Roe 1984a; 2. Roe, James, Thurston 1984; 3. Roe and Badcock 1984; 4. Torres and Childress 1983).

	Ascent		Descent
Systellaspis debilis[1]			
Adults	63.8		68.4
Juveniles	55.4		53.8
Gennadas elegans[1]	41.4		33.6
Atolla vanhoeffeni[2]	50		60
Euphausia krohni[2]		76	
Benthosema glaciale[3]	~100		~100
DSL in San Diego Trough[4] (probably *E. pacifica*)	60–270		
E. pacifica experimental[4] maximum		350	

To illustrate the approximate level of the fluxes, the daily migration of 1 gm fish per m^2 into and out of the surface 500 m at the eddy station can be used to estimate the fecal flux. If it is assumed that the daily ration is 10% of the body weight, the assimilation efficiency is 50%, the carbon content is 5% and all feces are voided at depth, then the fish alone will transport 2.5 mg C per day down out of the surface 500 m. This represents 0.4% of an annual production of 250 g $C \cdot m^{-2} \cdot y^{-1}$, and is in the form of material likely to sink out at over 1000 $m \cdot d^{-1}$. Most would be expected to reach the sea bed and would provide an additional input equivalent to 15–40% of the flux measured by sediment traps; a further 10–25% may originate from euphausiid and decapod feces. If these calculations are of the right order of magnitude, then vertical migration may have a significant effect on the sedimentation of organic material to the deep-living communities and on the chemical profiles of elements and compounds whose distributions are influenced by the organics. However, they are sensitive to variations in assimilation efficiency, so if an assimilation rate of 95% is assumed, as might occur for nitrogen, migrants will contibute an order of magnitude less to the downward transport. Hence shifts in the C : N ratios may provide useful insights into some of these processes. Evidence for rapid transport down deep water columns is beginning to emerge (e.g., Walsh 1983; Billett, Lampitt, Rice and Mantoura 1983), but it is not always easy to reconcile some of the carbon isotope data, particularly from the north Pacific, with such rapid transport (e.g., Pearcy and Stuiver 1983).

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EXPERIMENTAL APPROACHES TO THE STUDY OF VERTICAL MIGRATION OF ZOOPLANKTON

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ABSTRACT

The phenomenon of diel vertical migration by zooplankton was first noted more than 150 years ago. However, experimental studies of this behavior did not begin in earnest until the beginning of the 20th century. Early researchers quickly identified a number of factors which are still thought to play a role in controlling vertical migration: light, temperature, pressure, gravitation, and the requirement for feeding on phytoplankton. More recent studies have examined endogenous rhythms and avoidance of predation as potential controlling factors.

Despite the great effort expended on experimental studies of vertical migration, our understanding remains remarkably deficient. Many species have been studied, but few thoroughly. The behavior is not necessarily general since species may differ in their response to the same stimuli. The execution and interpretation of experiments are confounded by the multiplicity of controlling factors, in that such factors are usually studied one at a time, without regard to potential interactions. Finally, studies have been frustrated by the technical difficulty of recreating the appropriate scale (10's of meters) in the laboratory. The success of future studies will depend upon our abilities to systematically evaluate all potential controlling factors and their interactions, and to faithfully duplicate the real physical environment.

INTRODUCTION

The diel vertical migration of zooplankton is one of the most widespread, well-documented behaviors known to marine and freshwater biologists. Yet, after more than 150 years of field observation and 100 years of laboratory research, diel migrations remain an enigma. In this paper I seek to summarize the hypotheses and experimental results concerning the behavior, and attempt an assessment of the current state of our knowledge. I have limited the discussion to holoplankton, in both marine and freshwater systems. I have done so primarily to retain a continuity of scale; many marine animals perform vertical migrations during their larval stages, but these often occur in shallow, estuarine waters, a scale which differs greatly from the migrations of truly pelagic holoplankton.

Definition

Diel vertical migration is best defined as the vertical displacement of an individual, or group of individuals, which occurs with diel periodicity. Hutchinson (1967) defined three characteristic modes of migration: (1) ***nocturnal migration***, in which a single ascent is made from the day depth, with the animals coming closest to the surface between sunset and sunrise; (2) ***twilight migration***, in which ascents occur at both sunset and sunrise; and (3) ***reverse migration***, in which animals ascend during the day and descend during the night. Cushing (1951) considered twilight migration to be the most common pattern; reverse migrations are most rare.

Occurrence

Diel vertical migrations have been observed in every phylum represented in the marine and freshwater zooplankton. In the Protozoa, vertical migrations of Tintinnidae have been documented by Halme (1937). Many coelenterate medusae are known to make diurnal migrations (Russell 1925, Roe 1974); in a recent study their movements were monitored with an underwater videorecorder (Yasuda 1972). Observations of vertical migration in ***Pleurobrachia pileus*** off the coast of San Diego constituted the first such record among the Ctenophora (Esterly 1914). In the Polychaeta, migrations have been observed in ***Tomopteris*** (Russell 1928) and in the larvae of ***Mesochaetopterus sagittarius*** (Bhaud 1969). Migrations among the Chaetognatha have been frequently observed (e.g., Welsh, Chace and Nunnemacher 1937; Russell 1928; Pearre 1973; Roe 1974). Among the Mollusca, the giant squid (***Dodiscus gigas***) performs the most extensive migrations—more than 1000 m (Nesis 1970), but even the diminutive larvae of bivalves perform short migrations (Wood and Hargis 1971). In the Urochordata, vertical migration has been observed in the Pyrosomidae (Imber 1973) and Salpidae (Hardy and Gunther 1935; Wiebe, Haury, Harbison and Philbin 1979). Field observations of diel vertical migration in the Crustacea date back to Cuvier (1834), who first noted the behavior in freshwater Cladocera. Since then the records of migration among the Crustacea have been become too numerous to mention; for example, Bainbridge (1960) cited 156 species in which migrations had been documented.

The distances traveled by vertical migrators during the course of a diurnal cycle may vary from approximately 2 m, as in the case of copepod nauplii (Huntley and Brooks 1982), to approximately 1000 m, as for the euphausiid ***Thysanopoda acutifrons*** (Waterman, Nunnemacher, Chace and Clarke 1939) or the salp ***Salpa aspera*** (Wiebe et al. 1979). Many vertical migrators aggregate quite close to the surface at night, but most mesopelagic and bathypelagic migrants usually stay below the thermocline, ascending to not less than about 200 m. Day depths vary considerably, from several meters to more than 1000 m. An extreme case, noted by Banse (1964), is characterized by certain mysids known to live at 4000 m during the

day and to graze on surface phytoplankton at night. To further complicate the generality of the behavior, many species display different migration patterns within their life cycles and at different seasons.

Factors Affecting Vertical Migration

Observations of vertical migration of zooplankton had been made for more than 50 years before experimental studies began in earnest. Just before the turn of the century Groom and Loeb (1890) published their observations of "phototropism" (directed movement of an animal toward a light source, more correctly termed "phototaxis") in cirripede nauplii. Since then the effects of light and other factors have been tested in numerous experiments on many species of zooplankton.

The hypotheses advanced to explain vertical migration are almost as numerous as the migrators themselves. Yet, certain physical, chemical and biological factors have been recurringly identified as causative agents. These factors include (1) light, (2) pressure, (3) gravitation, (4) endogenous rhythms, (5) feeding or predation and (6) a variety of physico-chemical parameters such as temperature, salinity and pH. It is apparent that all these factors may influence vertical migration behavior, but their relative importance and the ways in which they interact remain significant objects of research.

METHODS

The sheer scale of most vertical migrations has demanded that experimentalists compromise their experimental design in one way or another. In field experiments the scale of the migration remains unperturbed, but one forsakes the ability to control variables. On the other hand, experiments conducted under controlled laboratory conditions usually forsake the true scale of the migration. Even the apparent compromise of using in situ enclosures or large-volume tanks has drawbacks. For example, the coefficient of vertical eddy diffusivity may be reduced by several orders of magnitude in an in situ enclosure relative to the surrounding waters (Steele, Farmer and Henderson 1977); it is difficult to determine what effect this virtual absence of turbulence might have on migration behavior.

Ideal experimental conditions can be approached with zooplankton species which do not make extensive migrations (e.g., many larvae, or *Daphnia* spp., both of which have been the subject of intensive investigation). However, it is difficult to assess the general applicability of results with such species.

Despite the limitations, many ingenious methods have been devised to study vertical migration, both in the laboratory and in the field. The "plankton wheel" developed by Hardy and Bainbridge (1954) deserves special mention here for two reasons. First, if a single example must be chosen, this one perhaps best represents the ingenuity of experimentalists. Second, experiments with the plankton wheel were intended primarily to determine vertical swimming speeds of plankton, rather than to examine the effects of various factors on controlling vertical migration behavior; thus

the device would not deserve mention elsewhere in this paper. The plankton wheel was essentially a perspex doughnut oriented in the vertical plane and able to rotate freely through the control of the experimenter, who could observe a vertical section of the wheel at eye level. After filling the wheel with seawater and plankton, the observer fixed his gaze on an animal in the field of view. Then, as the animal moved, the observer rotated the wheel, compensating for the animal's motion so as to keep it in the field of view. The motions of the wheel were recorded on a kymograph for later analysis. In this manner, Hardy and Bainbridge (1954) were able to demonstrate that the swimming velocities of individual plankton were compatible with the ascent of vertically migrating field populations.

I have used the example of the plankton wheel simply to demonstrate the ingenuity that is often required of experimentalists. In most cases it is more reasonable to discuss methodology in concert with the results obtained, and this is the approach I shall follow in the remainder of this paper. By piecing together the information from many independent experiments, I hope to present a current view of the factors which control diel vertical migration.

RESULTS AND DISCUSSION

Light

Crustacea—One of the first suggestions that vertical migration might be related to light intensity came from Weismann (1877). He believed that crustaceans performed daily vertical movements because their eyes were adjusted to a low intensity of light; the animals were suited to capturing food at night because it was the only time they could see their prey. However, Weismann's idea was pure conjecture, and he performed no experiments to test the hypothesis.

The first attempts to experiment with the effects of light on the movement of crustaceans were undertaken by Groom and Loeb (1890). They found that nauplii of ***Balanus perforatus*** show strong positive phototaxis upon hatching, but soon become negatively phototactic under the influence of intense light. However, they did not find that a sudden change in the intensity of light had any influence on the behavior of the nauplii. Ewald (1912), also working with ***Balanus perforatus***, found that a sudden increase in illumination inhibited locomotion and thus caused the animals to sink. Conversely, a decrease of illumination caused increased locomotory activity.

Extensive experiments with marine zooplankton were conducted by Esterly (1917, 1919). He enclosed a single animal in a stoppered, glass tube (50 cm × 3 cm) filled with seawater, which could then be maintained in either a vertical or horizontal position. His results were complex. For example, ***Acartia clausi*** and ***A. tonsa*** collected from the surface were positively phototactic, whereas those collected at depth were negatively phototactic. ***Calanus pacificus*** was negatively phototactic at "normal temperatures" but became positively phototactic at temperatures below 10°C, and similar results were obtained for ***Metridia lucens***. Esterly (1919) in his interpretation cautioned that "we should inquire whether reactions under controlled conditions in a

glass vessel are similar to those that would be observed...under otherwise natural surroundings." This comment remains true today.

In experiments with ***Daphnia***, Ewald (1910) found that animals moved in the vertical plane when lit from above but in the horizontal plane when lit from below. He concluded that locomotion was therefore parallel to the light gradient. He further reasoned that the animals had an "optimal" light intensity—a range of light intensities with upper and lower limits within which the animals prefer to remain.

The idea of an "optimal" light intensity has persisted for many years, but not without modification. Rose (1925) first elaborated upon the concept proposed by Ewald (1910), but he believed that phototaxis came into play only at the boundaries of the optimal range of light intensities. Unlike Ewald, who suggested that plankton undertook continuous movement in response to ambient light, Rose proposed that the animals were active only when there was sufficient deviation from the optimal light intensity.

Clarke (1930) conducted experiments with ***Daphnia pulex*** to examine "the fundamental mechanisms of phototropism in particular and of vertical migration in general." His experiments were performed with single animals contained in a glass tube (96 cm × 6.3 cm), with provisions for altering temperature and light. He showed that ***D. pulex*** was negatively phototactic to constant illumination but became positively phototactic when the light intensity was quickly reduced. Most importantly, he also observed that if the light intensity was reduced very slowly, no response occurred at all (i.e., the sign of the phototaxis did not change). From these results, Clarke deduced that there is a "relative optimum light intensity" to which animals are adapted at the moment, and he thus rejected the notion of an "absolute optimum" light intensity, which had been supported by Russell (1927).

Clarke (1933, 1934) took his hypothesis to sea. In a series of exhaustive field experiments, he took measurements at almost hourly intervals of the vertical distribution of ***Calanus finmarchicus***, ***Metridia lucens*** and ***Centropages typicus***, and of the daily cycle of underwater illumination to depths of more than 50 m. The results were not easily interpreted on the basis of the optimum light intensity theory. ***Calanus finmarchicus*** neither migrated consistently, nor did it remain within a reasonably narrow zone of light intensity. During the morning descent at one station, ***C. finmarchicus*** moved from the 1.0 $\mu W \cdot cm^{-2}$ isolume to the 0.01 $\mu W \cdot cm^{-2}$ isolume; during the evening ascent the copepods reversed their behavior, ascending again into light intensities a hundredfold greater. ***Metridia lucens*** was the most consistent migrator, but it apparently anticipated the change in light intensity when it began its ascent in the early afternoon. Clarke (1934) suggested that perhaps changes in light intensity acted merely "to initiate the emigration"; instead of actively following the optimum light intensity (phototaxis), the animals appeared to Clarke to respond to change in light intensity by simply initiating activity (photokinesis), and this activity ultimately resulted in upward motion.

Johnson (1938) confirmed experimentally that, for ***Acartia clausi***, the change in light intensity, and not the absolute light intensity, stimulates vertical migration. Schallek (1942) agreed that ***A. tonsa*** did not maintain itself within a range of absolute light intensities.

Hardy and Paton (1947) devised a unique method for performing vertical migration experiments at sea. They enclosed animals in a pair of 45 cm-long glass tubes, which were then lowered to various depths. After a short time a trap door in the center of each tube was closed and the proportions of animals in the upper and lower sections of each tube were compared. They observed that ***Calanus finmarchicus*** tended to move up at night and down during the day; using a mirror at the base of the tube, they showed that *C. **finmarchicus*** moved in response to light.

Cushing (1955) used the same device to study freshwater zooplankton and found that ***Diaptomus gracilis*** from shallow depths aggregated at the top of the tube, whereas those from deeper down moved to the bottom. This replicated Esterly's (1919) results with ***Acartia*** spp. However, Cushing found that several other species reversed their initial reactions with time, and so he concluded that light was the most important factor in vertical migration and that the animals' responses were photokinetic rather than phototactic.

The experiments of Harris (1953) and Harris and Wolfe (1955) with ***Daphnia magna*** reinforced the idea that light alone acts as the stimulus to vertical migration. Using a tall plastic tube (60 cm × 10 cm) containing a suspension of india ink, they were able to reproduce vertical migration cycles which followed closely the changes in light intensity. The cycles could be compressed into a period of about 2 h, so Harris and Wolfe (1955) suggested that no physiological rhythm is involved in vertical migration. Most importantly, their research showed that two independent mechanisms control vertical migration of *D. **magna***; the first is a photokinetic response which is responsible for the "dawn rise," the second is a phototactic response which orients the dorsal surface normal to light (frequently termed the "dorsal light reflex"). In a subsequent paper (Harris and Mason 1956), it was shown that *D. **magna***, whose eyes had been extirpated, continued to exhibit the photokinetic response but no phototactic response. Thus eyeless *D. **magna*** could carry out vertical migration determined only by light intensity.

Ringelberg (1964, 1966) presented strong evidence, based on a series of detailed experiments with ***Daphnia magna***, showing that it is the relative change in light intensity that causes phototaxis and subsequent vertical motion. He claimed that his results agreed with those of Clarke and Backus (1956) who showed that deep-scattering layers (DSL) did not follow absolute light intensity but rather moved into progressively higher light intensities during the afternoon. Ringelberg's reference to observations of deep-scattering layers is unfortunate for two reasons. First, observations of a DSL by Boden and Kampa (1967, p. 23) indicated that it did indeed follow the absolute light intensity ("the animals....seek to live, then, in a blue light within the narrow limits of 0.00035 and 0.00075 $\mu W \cdot cm^{-2}$"). Second, and more important, in the 1950's and 1960's DSL's were usually observed with 20 or 12 kHz echo-sounders, which are capable of identifying nekton, but certainly not plankton (for

which one requires much higher frequencies; see Holliday and Pieper 1980). Thus early observations of the movements of DSL's are not pertinent to zooplankton.

In the last two decades, little attention has been paid to the effects of light on marine crustacean zooplankton. No studies have resulted in a major advance of our understanding, in that they have failed to resolve the question of whether zooplankton respond phototactically or photokinetically and whether it is the absolute, the relative, or the change of light intensity which acts as the primary stimulus for movement. Even more disappointing is the fact that the bulk of what we know is based primarily upon studies of freshwater cladocerans; it is difficult to know if these results are applicable to marine crustacean holoplankton.

Chaetognatha—Vertical migration in chaetognaths was first observed by Michael (1911) who proposed that *Sagitta euneritica* maintained itself at "optimum" light intensities. Esterly (1919) performed experiments which demonstrated *S. euneritica* to be positively phototactic at low light intensities and negatively phototactic at high light intensities.

A host of later field observations established that vertical migration occurs in many chaetognaths, including *Sagitta elegans* (Russell 1928, Terazaki and Marumo 1979) and *S. setosa* (Russell 1928). Moore (1955) showed that nine species of chaetognaths vertically migrated in the Florida Current; the animals moved in the same direction as the isopleths of temperature and light intensity changed, but they "did not congregate at a depth corresponding to such a constant value." Pearre (1973) confirmed Esterly's (1919) results with *Sagitta elegans*, showing that phototaxis was positive at low light intensities and negative at high light intensities.

Pressure and Gravitation

Crustacea—The effects of pressure and gravitation are properly considered together because, in concert, they constitute the basis for another mechanistic model of vertical migration. This model, described succinctly by Rudjakov (1970), involves a period of passive, downward sinking attributable to gravity and a period of enhanced upward locomotory activity caused by increased pressure.

Early researchers (e.g., Esterly 1919) quickly adopted the notion of positive and negative "geotropism" (more correctly, "geotaxis," meaning active motion toward the center of gravitational force), and this terminology has unfortunately persisted. Given the manner in which experiments have been performed, it is often difficult to distinguish between downward movements caused by (1) negative phototaxis, (2) passive sinking or (3) positive geotaxis (which would imply an active behavior). In many cases, what has been called "positive geotaxis" (e.g., Esterly 1919, Clarke 1930, Harris 1953) could equally have resulted from passive sinking. Experimentalists have not yet subjected zooplankton to artificial gravitational fields, and until they do, a true geotaxis is difficult to demonstrate.

Rudjakov (1970, 1973) has clearly demonstrated that the downward vertical migration of many crustaceans could be due entirely to passive sinking. Measurements on anaesthetized individuals of 20 planktonic copepod species yielded sinking rates ranging from 1.8 to 47.4 $m \cdot h^{-1}$, with most species sinking at a rate of about 20 $m \cdot h^{-1}$. Rudjakov (1973) presented evidence to show that these rates are comparable with those observed in the field.

How could plankton animals regulate their position once they have sunk to their preferred depth? Angel (1970) showed that ***Conchoecia spinirostris*** can regulate its buoyancy without benefit of locomotory activity, but he could observe no obvious mechanism. Gooday and Moguilevsky (1975) also observed buoyancy regulation in nine other species of ostracods, but were forced to conclude that "the animals must be able to alter their density and hence buoyancy in some as yet undetermined way." Similar observations do not appear to have been made for the planktonic crustaceans.

A number of studies have documented an increase in locomotory activity or actual upward motion with an increase in pressure. Hardy and Bainbridge (1951) compared the swimming activity of zooplankton maintained at atmospheric pressure to those subjected to pressures equivalent to a depth of 20 m in 50-cm-tall perspex tubes. Striking results were obtained with zoea and megalopa larvae of the decapods ***Portunus*** and ***Carcinus***, but no effect could be demonstrated for ***Calanus finmarchicus***. Similar results were obtained by Knight-Jones and Qasim (1955) who detected upward swimming responses to increased pressure in two species of decapod larvae, the isopod ***Eurydice pulchra***, and the copepod ***Caligus rapax***. However, they failed to find a response in ***Calanus***. They suggested the pressure response was probably restricted to large crustaceans with high specific gravity. Rice (1964) found pressure-induced movements in zoeae of 22 species of decapods, and Maylor and Isaac (1973) found similar responses in megalopa of ***Macropipus*** sp. and ***Callinectes sapidus***.

Baylor and Smith (1947) found that very small pressure increases (< 1 atm) produced upward swimming behavior in many species of zooplankton from the Florida Inland Waterway, including ***Temora*** sp., ***Acartia***., ***Pontella*** sp. and ***Centropages*** sp. They eliminated the possibility that such behavior could have been caused by gas bubbles and noted that several minutes' exposure to pressures > 2 atm destroyed the pressure-sensitive mechanism.

George and Marum (1974) found that ***Calanus finmarchicus*** increased its swimming activity only at pressures corresponding to depths greater than 2000 m. Although *C. **finmarchicus*** does make seasonal migrations to about 1000 m, the pressure response observed by George and Marum does not suggest a mechanism for diel migrations of this species, which is usually found no deeper than several hundred meters.

Champalbert (1976, 1978) demonstrated that several species of pontellid copepods react to increased pressure by increasing their locomotory activity, but for them the response may function more to keep them in the surface waters than to control vertical migration since they are almost exclusively surface-dwelling forms.

Lincoln (1970, 1971) maintained ***Daphnia magna*** under constant overhead illumination and found them to respond to a pressure increase by upward movement; to a pressure decrease they responded with a downward movement. He concluded that the movements resulted from kinesis rather than from a directional taxis.

Other Taxa—Knight-Jones and Qasim (1955) found pressure-induced upward movements in three species of medusae: ***Phialidium hemisphericum***, ***Gossea corymetes*** and ***Eutima gracilis*** (Coelenterata). Baylor and Smith (1957) found a similar response at < 1 atm for an unidentified hydrozoan medusa. Knight-Jones and Qasim (1955) found an upward swimming response for ***Pleurobrachia pileus*** (Ctenophora) at approximately 0.05 atm, whereas Baylor and Smith did not observe a response below 0.7 atm.

Sagitta spp. (Chaetognatha) are also known to increase activity in relation to pressure increases, but the response appears variable. Baylor and Smith (1957) found a response at 0.7 atm, George and Marum (1947) found a response at 35 atm, and Knight-Jones and Qasim (1955) found no response. The pelagic tunicate ***Salpa fusiformis*** increases its activity level at approximately 100 atm (George and Marum 1974).

Endogenous Rhythms

The possibility that an internal physiological rhythm might control vertical migration behavior has been raised by a number of investigators. The persistence of vertical migration behavior in the absence of light stimuli was first noted in ***Acartia*** spp. by Esterly (1917) who claimed to observe an ascent which began between 0600–0800 h and a descent which occurred between 2000–2100 h. These results suggested a reverse vertical migration, which was consistent with Esterly's (1919) observations on ***Acartia*** spp.

However, there were problems with Esterly's experimental methods. First, he occasionally used white light to locate and count copepods within his experimental cylinder, which light could have influenced the distribution of the copepods. Second, he commented that "on account of the mortality among the animals, there is not much that can be said about the duration of the tendency to ascend at certain times." Experimental errors aside, Esterly's conclusions regarding endogenous rhythms are questionable since he failed to observe the copepods between 2100 and 0800 h.

Schallek (1942) attempted to replicate Esterly's (1917) results with ***Acartia***; he reduced mortality by feeding the copepods at random and, unlike Esterly, he used a 25 W red lamp to locate the copepods kept in otherwise constant darkness. Schallek never found the rhythm reported by Esterly, concluding that "no evidence was found for a diurnal rhythm other than that caused by the normal alternation of day and night. Migration ceases under constant conditions; it can be reversed by illuminating the animals at night and keeping them in the dark by day." Conover (1956) also repeated Esterly's (1917) experiments but, like Schallek, found no evidence of a biological rhythm in ***Acartia tonsa*** kept in constant darkness.

Harris (1963) observed endogenous rhythms in *Daphnia magna* and *Calanus helgolandicus*. He observed that in *Calanus* the rhythm did not occur in winter months, when this copepod typically does not vertically migrate (Nicholls 1933). Rimet (1960) made similar observations on *Daphnia pulex* but found that the rhythm dissipated entirely after 3–4 days. Champalbert (1978) also found, in three species of pontellid copepods, a circadian rhythm which disappeared after 3–4 days under constant conditions.

Enright and Hamner (1967) filled a 5-m-deep, 170-m^3 tank with a mixture of field-collected zooplankton, subjected them initially to a light-dark cycle for several days, and then maintained constant, low light conditions for a period of days. Surface samples taken at regular intervals showed that several species (*Nototropis* sp., *Exosphaeroma* sp., *Cyclaspis* sp. and peltidiad copepods) continued to make synchronized vertical migrations under the constant conditions, and these movements were attributed to endogenous rhythms. However, a number of species did not yield evidence of an endogenous rhythm notably *Acartia* spp.—in which Schallek (1942) and Conover (1956) also failed to find such a rhythm.

Feeding and Predation

Crustacea—Although the connection between vertical migration and feeding was suggested long ago (Weismann 1877), it was only recently that experimental studies were undertaken to examine this relationship. Hardy and Gunther (1935), noting the inverse relationship between zooplankton and phytoplankton in Antarctic waters, proposed that dense concentrations of phytoplankton might produce exocrine substances which would exclude zooplankton herbivores from the region. It is interesting that they chose this hypothesis since the distributions they observed could be explained equally well if one assumed that low concentrations of phytoplankton were a result of grazing by the zooplankton. There is some evidence that herbivorous zooplankton will avoid high concentrations of phytoplankton on which they are not grazing (Fiedler 1982), but because herbivorous zooplankton require phytoplankton for sustenance they are unlikely to avoid them on a routine basis.

Since many herbivorous vertical migrators are situated below the photic zone during the day, they must feed in surface waters at night. Feeding may continue in surface waters until increased light intensity causes the animals to descend. This view is supported by the experimental results of Clarke (1932) who found *Daphnia* to be more photonegative when fed than when starved. Similar results have been obtained for *Eurytemora hirundoides* and *Neomysis* (Lucas 1936), as well as for barnacle nauplii (Singarajah, Moyse and Knight-Jones 1967).

Many recent studies of vertical migration and feeding have been conducted in the field. Such a study performed on *Mysis relicta* demonstrated that the animals experienced an increase in their caloric content during their nightly excursion into the surface waters of a lake in Wisconsin (Teraguchi, Wissing and Hasler 1972). Grossnickle (1979) used gut pigment analysis to arrive at the same conclusion for *M. relicta* in Lake Michigan. Gut content studies of *Pseudocalanus elongatus* in the

Black Sea showed a distinct nocturnal feeding rhythm associated with diel migration (Zagorodnyaya 1975); similar results were obtained under experimental conditions. Analogous results have been found for field populations of ***Parathemisto japonica*** (Zhuravlev and Neyman 1976), ***Pseudodiaptomus hessei*** (Hart 1977), ***Calanus glacialis*** (Peruyeva 1978), ***Calanus helgolandicus*** (Gauld 1953), ***Calanus finmarchicus*** (Gauld 1953), ***Euphausia diomedeae*** (Ponomareva 1971), ***Thysanopoda*** sp. (Hu 1978), and a number of copepods from the Pacific Central Gyre (Hayward 1980).

Boyd, Smith and Cowles (1980), working off the coast of Peru, used the phaeophytin gut contents of three copepod species to quantify their feeding behavior. They found complex feeding patterns. ***Calanus chilensis*** fed throughout the day and night at onshore stations but fed only during the day at offshore stations. ***Centropages brachiatus*** fed day and night onshore but fed only at night offshore. ***Eucalanus*** spp., which vertically migrated at the onshore station and fed only during the day, were nonmigratory offshore but also fed only during the day.

Haney and Hall (1974) made in situ measurements of clearance rate and vertical migration in ***Daphnia*** spp.—one of the few attempts to make in situ measurements of feeding activity. They showed that ***Daphnia*** fed by night, at a time corresponding to their residence periods in surface waters.

More recently, Huntley and Brooks (1982) conducted a 60 d experiment in a 10-m deep, 70 m^3 tank, using the copepod ***Calanus pacificus***. They demonstrated a relationship between vertical migration and the abundance of available phytoplankton food. When food was abundant and ingestion rates were high, the copepods performed high amplitude vertical migrations. By contrast, when food availability declined, ingestion rates were low and the copepods remained at the surface throughout the day. Similar results have been obtained for ***Pseudocalanus*** (Bohrer 1980). Huntley and Brooks (1982) suggested that such results might explain daytime surface swarming observed in ***Calanus*** during summer periods when food availability is low (e.g., Marshall and Orr 1927, Bigelow 1926).

Rather than regarding daytime descent as a purely passive event (cf. Rudjakov 1970), some researchers have proposed that the descent is an evolutionary adaptation for the purpose of avoiding visually orienting predators (Zaret and Suffern 1976). A field study of ***Calanus pacificus*** was conducted by Enright and Honegger (1977) to examine this hypothesis, but their results were inconclusive. The strongest support for this hypothesis comes from a recent study by Ohman, Frost and Cohen (1983). They demonstrated that reverse vertical migratory behavior developed in ***Pseudocalanus*** when the copepod's predators (***Euphausia pacifica***, ***Euchaeta elongata*** and ***Sagitta elegans***), which vertically migrated in the "normal" pattern, became abundant. When these predators were not abundant, ***Pseudocalanus*** performed a normal, nocturnal vertical migration.

The question of whether or not vertical migration can be an adaptation for the avoidance of grazing pressure, or indeed simply a functional response to predation pressure, is far from being satisfactorily resolved. Predators which feed at the surface at night apparently take advantage of nocturnally migrating zooplankton prey, as has

been observed, for example, in the grey-faced petrel, which feeds exclusively on vertically migrating zooplankton species coming into the surface at night (Imber 1973). In this case, it can be argued that the predator has evolved its nocturnal feeding habits as a consequence of the behavior of the zooplankton migrants. It may be the sum total of predation pressure which is important in this regard (i.e., one or two specialized predators may not have enough impact to reverse the normal, nocturnal migrations of an entire zooplankton community).

Chaetognatha—A landmark study on the relationship between feeding and vertical migration was conducted by Pearre (1973). His observations of the vertical distributions of ***Sagitta elegans*** showed no apparent vertical migration behavior. However, further analysis showed that animals caught at the surface always had a greater amount of food in their guts than animals at depth, and he concluded that the requirement for feeding was the motivating factor in vertical migration. In a later study, Pearre (1979) argued convincingly that conventional sampling methods can only detect synchronous migrations.

A recent study of ***Sagitta nagae*** (Nagasawa and Marumo 1976) found that this species feeds both in surface waters and near the bottom in Suruga Bay, Japan. However, feeding in the surface is greatest at night, whereas feeding near the bottom is greater during the day.

Other Exogenous Factors

While physical factors such as salinity, pH and temperature have not been shown to directly control vertical migration, they have often been shown to alter the response of zooplankton to light or to limit the extent of migrations. For example, Loeb (1906, 1908) demonstrated that plankton become positively phototactic at high concentrations of CO_2, whereas they become negatively phototactic at decreased salinities. Esterly (1919) showed that temperature decreases caused negative phototaxis in ***Acartia*** and positive phototaxis in ***Calanus*** and ***Metridia***.

Loeb (1908) described a complex model of vertical migration that depended upon diel changes in temperature and pH, but the importance of these factors in the field has since been refuted by a number of investigators (e.g., Moore 1955, Hardy and Paton 1947, Ringelberg 1964, Bainbridge 1960). Bayly (1963) suggested that reverse vertical migration was characteristic of zooplankton in fresh waters of pH 8.2 or higher, and Connell (1978) has presented additional evidence in favor of this hypothesis. However, the importance of pH in altering the vertical migration of marine zooplankton remains questionable; seawater is well buffered and most changes in pH are due to increases in alkalinity attributable to high rates of photosynthesis.

SUMMARY

Light is perhaps the single most important factor to influence vertical migration, but the mechanism of its action remains poorly understood. Does a reduction in light intensity directly induce locomotory activity which causes plankton to move upward? Or does it simply act as a "zeitgeber," a cue which enacts an endogenous activity rhythm or a hunger response?

It is attractive to consider that vertical migration behavior could be accounted for entirely by the combined effects of pressure-induced upward swimming and gravity-induced, passive downward sinking. Certainly, abundant data exist to indicate the existence of such a mechanism. However, observed sinking rates are often so high that the question remains as to what stimulates the zooplankton to stop sinking. A mechanistic model based upon pressure and gravitation requires an additional cue, such as light or hunger, to provide the timing to properly synchronize the circadian nature of the migration.

Endogenous rhythms have sometimes been implicated in vertical migration behavior. However, these rhythms often decay with time in the absence of external stimuli, so synchronization stimuli are necessary adjuncts to the internal rhythm. Furthermore, many vertical migrators do not appear to possess internal timing mechanisms of this type.

The connection between feeding and vertical migration requires further research. There is some evidence that well-fed zooplankton descend with the advent of daylight. However, do they descend because of a simple increase in their specific gravity (Eyden 1923), because they are satiated, or because satiation causes negative phototaxis? As far as the vertical ascent is concerned, there has been no experimental study examining its relation to hunger or requirement for feeding.

The importance of vertical migration as a functional response to predation is not well understood. Experimental studies designed to test this hypothesis are difficult to perform, and few have been undertaken. Of the few such studies done, the results have been equivocal.

The role of other physico-chemical factors such as temperature, pH and salinity appears not to be a major one. At best, these factors may act as modifying influences, but do not exert overriding control.

Future Studies

The numerical abundance of planktonic Crustacea in aquatic environments has understandably made them the center of attention in vertical migration studies. However, most of what we assume to apply to marine crustaceans results from studies of freshwater Cladocera, the most intensively studied group of Crustacea. In the case of light stimuli, for example, it is studies on cladocerans ***alone*** that have revealed the existence of color dances (Baylor and Smith 1957), the dorsal light reflex, and polarized light responses (Waterman 1973). More studies are required on marine crustacean holoplankton, and other planktonic groups, about which we still know very

little.

The design of future experiments will continue to tax the ingenuity of biologists. The admonition by Pearre (1979) that conventional sampling methods can only detect synchronous migrations of field populations calls for the use of additional measurements in conjunction with studies of distribution. The trade-off between true scale and the control afforded by laboratory conditions remains a problem. However, recent technological advances in automatic monitoring devices (e.g., video or high-frequency acoustics), as well as in techniques of underwater observation, make it possible to improve the frequency and the quality of observations in both field and laboratory experiments. Finally, one cannot neglect the power of pencil and paper, an approach which Vlymen (1970) proved useful in calculating the energy expenditures of migrating copepods.

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ADAPTIVE VALUE OF VERTICAL MIGRATION: COMMENTS ON THE PREDATION HYPOTHESIS AND SOME ALTERNATIVES

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ABSTRACT

Four main hypotheses address the diel vertical migration of zooplankton: an energetic and demographic hypothesis, a metabolic and photosynthesis hypothesis, a predator avoidance hypothesis, and a photodamage hypothesis. The energetic and metabolic arguments are seriously weakened by temperature effects. Both underestimate the influence of temperature on egg development and maturation, an important error which complicates metabolic arguments. In contrast, the predation and photodamage hypotheses provide reasonable, straightforward reasons why zooplankton should descend at dawn and rise again at dusk.

With regard to past reservations about the predation hypothesis, many of the original concerns are no longer justified. Studies of pigmentation, bioluminescence, and chemical defenses are clearing up several of the suspected exceptions. Yet in future studies, the predation hypothesis should be framed in a more comprehensive way, as risk from predation (differential survivorship) balanced against the advantage of remaining in place to exploit resources (differential reproduction). Viewed from this perspective, vertical migration becomes an excellent example of an evolutionary compromise.

INTRODUCTION

The daily vertical migration of zooplankton is so commonplace in marine and freshwaters that there is a tendency to take the phenomenon for granted. At least 15 phyla contain one or more species known to migrate, with individual cases that span the range of physical and chemical parameters (e.g., salinity, temperature, depth). Yet the widespread pattern should not imply common inheritance of a conservative evolutionary trait. Diel vertical migration seems to have evolved independently in many taxonomic groups. The argument for polyphyletic origin is strengthened by three observations: (1) certain species do not migrate, although other taxonomically and ecologically similar organisms do, (2) some species migrate during one season, or in one location, but not in others (i.e., time and spatial incidence is variable), and (3) only certain life stages may migrate, typically the older instars (Enright 1977). These peculiarities suggest a major selective advantage for diurnal vertical migration, although there is still considerable controversy over both the nature of the response and the reasons for its widespread occurrence.

Research on the subject of diel vertical migration has developed along two distinct lines. One presently focuses on the neurophysiological basis of the behavior, dealing with the so-called proximate factors. Proximate factors are the stimuli that initiate the response, that determine direction, and that govern speed of the migrating organism. These releasing, orientation and directing stimuli often involve complex feedbacks. For example, in *Daphnia* the initiating stimulus is a change in light intensity relative to the prevailing absolute intensity (Clark 1930, Ringelberg 1964, Ringelberg et al. 1967), while the directing stimulus appears to be an optical beacon, at least in shallow waters (the so-called Snell's window; See Ringelberg 1964; Siebeck 1960, 1968, 1980; Siebeck and Ringelberg 1969). However, this well-researched and elegant example should not imply that all organisms or even the majority of microcrustaceans use identical cues. Because the origin of diel vertical migration is polyphyletic, there is no reason to suspect the same proximate cues in every case.

The other line of research concerns the teleological considerations of purpose and design (Ringelberg 1980a). As mentioned previously, the wide-spread occurrence of a polyphyletic pattern suggests an adaptive value to the behavior. Yet care must be taken to avoid excess speculation. Because evolutionary arguments invoke natural selection as the process that molds behavior and morphology, hypotheses require an even broader context than is often necessary for investigation of proximate factors. The question of inheritance and the overall impact of factors upon fecundity and survivorship are necessary elements in any complete argument. With respect to inheritance, there is little debate that natural or laboratory selection can modify reaction of organisms to proximate stimuli (e.g., Banta 1919, Banta and Wood 1928). Arguments based on natural selection require demographics, however, and there is heated disagreement over which aspects of fecundity or survivorship favor diel vertical migration.

The study of adaptive significance is complicated by a further consideration, the broad definition of diel vertical migration. Daily vertical displacement is such a commonly observed behavior and the taxa in which it occurs so diverse, that it is highly unlikely that one hypothesis applies to all cases. At least over the entire range of taxa, the phenomenon undoubtedly involves several contributing factors, i.e., a situation of multiple causation (Cushing 1951, Hutchinson 1967). For example, while not considered further in this paper, avoidance of periodic currents is an important, yet site-specific factor which can influence zooplankton behavior in estuaries or over banks. Faced with the realization of multiple causation, efforts should specify the taxa covered by a particular hypothesis, and concentrate on hypotheses that are both general and testable.

In this paper I address the adaptive value of diel vertical migration in zooplankton with special attention to the strengths and weaknesses of several leading theories. Certain exceptions are examined to see if they really contradict or actually support the central thesis. The overall approach taken is partly synthesis and partly critical evaluation, since in some cases recent discoveries have resolved particularly perplexing dilemmas (e.g., bioluminescence of migrating organisms), whereas in others they have only contributed to a better definition of central questions (e.g., why should herbivores move away from resources).

MAJOR HYPOTHESES FOR PELAGIC ZOOPLANKTON: STRENGTHS AND WEAKNESSES

At present, there are four major hypotheses to explain why so many organisms should show the basic diel vertical migration pattern of down during the day and up during the night. The central question is why herbivores should move into deeper waters during the daytime, away from the regions of maximum plant biomass and photosynthesis. At higher trophic levels there are additional complications as omnivorous and predatory invertebrates are expected to respond both to the migrations of their resources and to encounter risks from predators (Gerritsen 1980). For herbivores, however, the critical evolutionary question involves sacrifice, i.e., what benefit compensates for the reduced food intake during daylight hours or what risk causes organisms to flee from their feeding grounds? All these hypotheses generally pertain to zooplankton approximately 0.5−100 mm body length, with emphasis upon microcrustaceans. The four, listed by either their author or most recent proponents, are:

1. An energetic and demographic hypothesis which postulates a benefit of cool temperature to metabolism, growth, and fecundity (McLaren 1974);
2. A metabolism and photosynthesis hypothesis which couples a cool-water metabolic advantage with migration timed to crop the daily peak of primary production (Enright 1977);
3. A predator-avoidance hypothesis which advocates light-dependent diel migration to avoid visual predators (Murray and Hjort 1912, Zaret and Suffern 1976, Stich and Lampert 1981);

4. A photo-damage hypothesis which directly links survivorship with avoidance of short-wave irradiation (Huntsman 1924, Hairston 1976).

From the perspective of population dynamics, all four arguments attempt to maximize r in the relationship

$$1 = \sum e^{-rx} \cdot l_x \cdot b_x \tag{1}$$

The first two hypotheses emphasize fecundity as the primary source of gain, whereas the latter two deal almost exclusively with survivorship. The thermal-efficiency aspect of both hypotheses 1 and 2 assumes that although the organism leaves a region of high food availability and descends into a region of reduced food quantity and quality, the processing of food and basic metabolism are aided by lower temperatures. This benefit then translates into larger adult size and consequently potentially greater fecundity (McLaren 1974). The second hypothesis more directly addresses the diel pattern and brings up the interesting question of fortuitous benefits associated with periodic resource release and cropping. However, a basic flaw in both hypotheses 1 and 2 is how temperature modifies demographic variables.

METABOLIC HYPOTHESIS

Surprisingly, McLaren (1974) acknowledged the weakness in the very paper which proposed his hypothesis when he stated "increased fecundity from low temperatures does not compensate for retarded maturation in determining potential rate of increase." The McLaren model minimized developmental effects because it: (1) allowed nauplii and early copepodite instars to remain in the warm epilimnion, (2) required only the III−V instar copepodite stages to migrate, and (3) allowed the adults to return to the epilimnion and to remain there throughout brood production. The third assumption, which is contrary to most observations of vertically migrating species (i.e., large, egg-bearing females commonly show the greatest amplitude of vertical movement), insured that females were in food-rich environments during their reproductive period and that both brood and egg development followed the warm schedule.

While there may be slight advantages in body size or brood size associated with periodic excursions into regions of cooler water, laboratory and simulation studies have failed to document an overall advantage to this behavior without additionally considering survivorship. Either energetic models have suggested little or no benefit (Swift 1976, Giguere and Dill 1980) or more comprehensive demographic simulations have shown no advantage (Wright et al. 1980, Orcutt and Porter 1983). Carefully conducted laboratory and field studies with *Daphnia* likewise have failed to show an overall reproductive advantage to vertical migration (Orcutt and Porter 1983, Stich and Lampert 1981). At the heart of these failures is a fundamental relationship between temperature, brood size, and the instantaneous birth rate that seriously undercuts both hypothesis 1 and 2.

Ever since the classical works of Leslie (1945, 1948), Cole (1954), and Lewontin (1965), the connection between brood sizes and the instantaneous rate of population growth (r) has been recognized as nonlinear. Working from Leslie's equations which relate finite and instantaneous birth rates, Paloheimo (1974) provided an exact solution for the particular case of egg-carrying organisms. The Paloheimo derivation makes the conventional assumptions of constant birth rate, constant death rate, and fixed development time. In addition, it assumes that because eggs are carried by female parents until hatching, the eggs are subject to the same mortality schedule as adults (the latter assumption is occasionally violated in nature, e.g., when adults drop eggs). Under the Paloheimo conditions, the instantaneous birth rate (b) is related to the number of eggs carried by females ($\bar{E}$) by:

$$b = \frac{\ln (\bar{E} + 1)}{D} \tag{2}$$

where D is the developmental duration of the eggs. This equation is widely used in limnological research and has received independent field verification (Polishchuk and Ghilarov 1981, Lynch 1982). Given that the egg ratio is the product of the average number of eggs carried by adults ($\bar{E}_A$, adult egg ratio) and the fraction of adults in the population ($\bar{E} = f_A \bar{E}_A$), an exponential increase in fecundity is necessary to compensate for developmental lags associated with movement of individuals into regions of decreased temperature (Fig 1, Table 1). While the specific growth rate of a population (r) is equal to the difference between instantaneous birth (b) and death (d) rates,

$$r = b - d, \tag{3}$$

r is a convenient measure of clonal fitness in parthenogenetic species such as *Daphnia* (Orcutt and Porter 1983). If, for the sake of argument, d is presumed constant, r would basically reflect the dynamics of the instantaneous birth rate. Under these conditions the greater the temperature differential between epilimnetic and hypolimnetic waters, the less likely that fitness of migratory clones could keep pace with that of nonmigratory clones.

Although admittedly simple, the relationship given in Figure 1 answers the question, What reproduction is necessary for a migrating *Daphnia* clone to keep pace with one which remains in place? In this particular example, the nonmigratory clone is assumed to inhabit a 20°C epilimnion, be composed of 30% reproductive adults ($f_A = 0.30$), and have a birth rate of $b = 0.15$. Given the listed values for D, taken from known laboratory values, and assuming *Daphnia* spend half their time each day in the cool hypolimnion, the $\bar{E}_A$ and $\bar{E}$ are then calculated to keep pace with the b of the nonmigratory clone. With a temperature difference of only 5°, a 46% increase in fecundity is necessary to compensate for the effect of temperature. If the difference reaches 15°C, a 7.7-fold difference is necessary. Since the *Daphnia* are moving away from their food supply, it is difficult to reconcile these differences without invoking compensatory adjustments in survivorship.

While the influence of temperature upon developmental time undercuts a central element of both the McLaren and Enright hypotheses, this flaw should not divert attention away from the marked dissimilarities of the two models. The McLaren hypothesis incorporated four assumptions: (1) food was available in excess; (2)

Table 1

Increase in the reproduction of a migrating *Daphnia* clone in order to compensate for the effect of temperature on development. Variables include: (1) temperatures of various water strata(°C) and difference (ΔT) in temperature between surface (20°C) and lower strata, (2) instantaneous birth rate (b) and frequency of mature adult females (f_A), both fixed, (3) developmental durations for eggs (D_{strata}, if remained in strata; D_{AV}, average between 20°C and lower stratum), and (4) egg ratio for population ($\bar{E}$) and for mature females ($\bar{E}_A$). Model uses the relationship:

$$b = \frac{\ln(\bar{E} + 1)}{D}$$

to ask the question, What value of $\bar{E}_A$ is necessary to maintain b at a value of 0.15, given $\bar{E} = f_A \bar{E}_A$, $f = 0.30$, and D values appropriate for *Daphnia*? Model assumes 50% of time spent in 20°C epilimnion, 50% at depth of lower temperature.

Clone	Temp	ΔT	b	f_A	D_{strata}	D_{AV}	$\bar{E}$	$\bar{E}_A$	$\bar{E}_A$ (*Mig*) / $\bar{E}_A$ (*Nonmig*)
Nonmigratory	20°C	0°	0.15	0.30	2.60	–	0.48	1.60	1.00x
Migratory	15°C	5°	0.15	0.30	4.50	3.55	0.70	2.33	1.46x
Migratory	10°C	10°	0.15	0.30	9.40	6.00	1.46	4.87	3.04x
Migratory	5°C	15°	0.15	0.30	18.00	10.30	3.69	12.30	7.69x

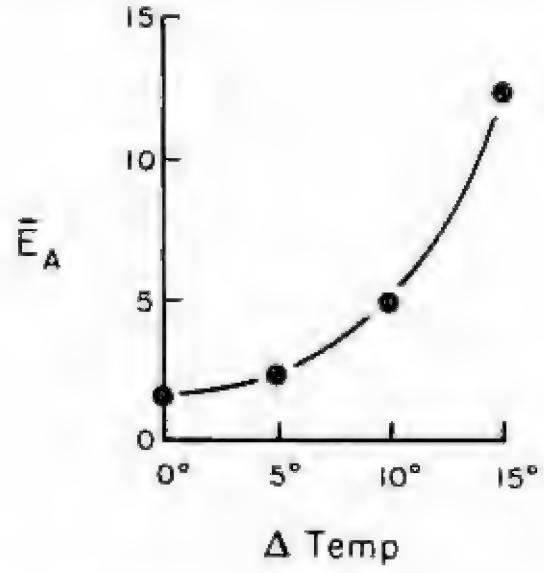

Figure 1

Increase in adult egg ratios ($\bar{E}_A$) necessary to offset developmental delays associated with vertical migration (see Table 1 for details).

population growth was at or near equilibrium, presumably through predation loss; (3) juvenile mortality was high relative to adult mortality; and (4) migration required negligible energy expenditure. The disclaimer on food limitation, which is also a part of an earlier version of the energetic hypothesis (McLaren 1963), has no support from careful field studies. In almost all detailed investigations of freshwater zooplankton dynamics, the major decline in fecundity from spring to late summer is primarily resource-related (Lampert 1978, DeMott and Kerfoot 1982). This can be dramatically demonstrated by enriching the natural phytoplankton with highly edible laboratory algae at the same biomass as the summer low-quality resources (e.g.,

Chlamydomonas, see Kerfoot and DeMott 1980). The presumption of excess food served to direct attention away from the serious question of how migrants compensate for food gained by nonmigrants. Furthermore, relaxation of food limitation begged the question of what limited population growth and shifted interest away from critical considerations of density-dependent resource interactions (e.g., intra- and interspecific competition).

In marked contrast, the Enright hypothesis focused attention on the energetic feedbacks between grazers and their resources. Although earlier workers had recognized a potential benefit to phytoplankton if grazers periodically left illuminated upper waters (McAllister 1969, Kerfoot 1970), the Enright model was the first attempt to couch interactions in the rigorous framework of an individual adaptive strategy. The model made several assumptions: (1) that photosynthesis could increase algal biomass appreciably from dawn to dusk, (2) that the metabolic needs of grazers could be reduced by individuals resting dormant during nonfeeding hours in cool, deeper waters, and (3) that an accelerated rate of feeding by returning grazers could partially compensate for the reduced daytime feeding. Although the model failed to incorporate temperature effects upon development and did not directly address density-dependent considerations of competition, it opened the door to a host of important questions. Among the most important were resource-related inquiries: to what extent were migrants and nonmigrants limited by resources? Did the density changes associated with mass displacements of entire migrating communities imply periodic release and depression of phytoplankton populations? Was there a fortuitous consequence of vertical migration to phytoplankton assemblages and enhanced stability to consumers (i.e., arising from inability of consumers to overexploit resources)?

VISUAL PREDATION HYPOTHESIS

The visual predation hypothesis has a long history of casual mention and is indirectly tied to the photodamage hypothesis through such subjects as pigmentation and transparency. Yet the technical treatment is largely one of historical neglect. As recently as 1963, McLaren could state the central theme and remark

> The upper waters are food-rich, but dangerous by day; herbivores are forced to secure their food there by night, and carnivores, if they themselves are not likewise prey, follow the behavior of their food species. Although this idea has had a long history and is still current..., it has received remarkably little attention or support from most of those who have reviewed the subject at large.

Back in 1963, outspoken reservations focused on what seemed to be embarrassing exceptions. These will be mentioned later. At the basis of the visual predation hypothesis, however, was an undeniable fundamental difference between terrestrial and pelagic environments. One of the most important aspects of predator-prey interactions in terrestrial environments is the presence of physical cover or refuges. These structural elements are absent from the pelagic zones of most lakes and open-water marine regions. Prey organisms are exposed to visual predators during the daytime in the euphotic zone (Murray and Hjort 1912, Zaret and Suffern 1976, Lythgoe 1979). In a sense, they are naked.

In freshwater ecology, the visual predation hypothesis fits nicely into a recently expanded awareness of how fish predation influences zooplankton community structure. Ever since the pioneering work of Hrbácek and his associates in Czeckoslovakian waters (Hrbácek 1962, Hrbácek and Novotná-Dvoráková 1965) and the publication of the more popular size-efficiency hypothesis (Brooks and Dodson 1965), fish predation has played a progressively greater role in models of zooplankton community interactions. Both descriptive and experimental studies convincingly document that freshwater fishes can profoundly alter the nature of pond and lake assemblages by excluding large-bodied and conspicuous species and by favoring small-bodied or transparent species. Recent summaries are found in Hall et al. (1976), O'Brien (1979), Zaret (1980), and Kerfoot (1980a). As an explanation for diel vertical migration in freshwaters, visual predation has exceptional appeal because it offers such a simple and straightforward explanation for so many attributes:

1. Timing: Visual predation provides a simple reason why zooplankton should descend at dawn, yet rise again at dusk.
2. Body Size: Large-bodied, active species should migrate more than small-bodied or inconspicuous species.
3. Ontogeny: Larger, older instars should migrate more strongly than smaller, younger instars. Egg-bearing adults should show the greatest amplitude of migration, because eggs or embryos often increase conspicuousness (Zaret and Kerfoot 1975, Bohl 1982, Vuorinen et al. 1983).
4. Spatial and Temporal Heterogeneity: Migration should be most likely when and where risk is greatest. The density and activity of planktivorous fishes varies greatly on both a seasonal, local, and latitudinal scale.
5. Transparency: Because transparent prey are better concealed, they should show less migration than pigmented species of similar body size.

Not only is the visual predation hypothesis compatible with the established view of fish impact on freshwater community structure, both laboratory and field tests on vertical migration demonstrate its reasonableness relative to alternative explanations (Zaret and Suffern 1976, Wright et al. 1980, Stich and Lampert 1981). In at least one case, there is even historically documented evidence to link the onset of vertical migration in a single species with an abrupt increase in fish density (***Mesocyclops***, Williamson and Magnien 1982).

In marine systems, given the logistical difficulties of conducting experiments, direct evaluation of the visual predation hypothesis is much more difficult. Yet the study of visual predation and prey adaptations is a well-developed field (e.g., Lythgoe 1979). For those accustomed to diving in open-water expanses of the ocean, the feeling of vulnerability is acute. To quote Hamner (1976)

> Animals in the euphotic zone...simply cannot hide during the day. In a sea devoid of cover...the visual acuity of the predators, and the size, speed, and transparency of prey all become critical, and the over-riding importance of visual predators for the evolution of all members of this ecosystem is particularly clear.

According to Hamner and his associates (Hamner et al. 1975, Hamner 1976), pelagic organisms fall into four general categories: (1) animals that are either too small to be seen or just too small to excite the interest of particular visual predators (visual predators may include species other than fish, e.g., invertebrates such as squid), (2) animals that are large but transparent enough to be invisible to visual predators, (3) animals that are large and readily visible, but that either congregate in schools for safety (e.g., herring) or are fast and predatory (e.g., sharks), and (4) animals that are nocturnal, and that seek cover through vertical diel migration (e.g., euphausiids).

In freshwater and marine environments, the important variables in the planktivore-grazer interaction are nearly identical. Grazer fecundity largely depends on animals feeding where algal density and productivity are greatest, i.e., in the euphotic zone. Risk from visual predation depends on predator density and movement, light intensity, prey density, and individual conspicuousness. Finally, dependence on light implies that predation efficiency will potentially be greater higher in the euphotic zone and at midday.

Taking the above variables into account and applying game theory to maximize both predator and prey fitness, Iwasa (1982) produced a simple diel migration pattern with some intriguing consequences. Visual predation rate attained its maximum shortly after sunset and before sunrise, while the community grazing rate was higher during the night than during the day. One additional appealing result was a clear statement of dependence on grazer survivorship ***and*** birth rate. Increased tendency for migration was related not only to the feeding intensity of fish, but also to the scarcity of phytoplankton since food through ***b*** and mortality through ***d*** simultaneously determine ***r***. Hence seasonal variation in vertical migration may relate as much to zooplankton birth rate as to predator pressure (see data in Kozhov 1963, Cunningham 1972, Stich and Lampert 1981).

The usefulness of demographics in field studies is also illustrated by two recent works. One considers the reverse migration of prey which respond to the conventional diurnal migration of large invertebrate predators. This well-documented case concerns the vertical migration of ***Sagitta***, ***Euphausia***, and ***Euchaeta*** to avoid fish predation (Pearre 1973). Migration of these invertebrate predators sets up a reverse migration in the herbivorous copepod ***Pseudocalanus*** (Ohman et al. 1983). Using the laboratory data of McLaren combined with a simple encounter model, Ohman et al. calculated that a mere 16% reduction in mortality would favor migration of ***Pseudocalanus***, whereas the actual benefit was closer to 50%. The second case suggests even greater benefits. In the ***Daphnia*** data set published by Stich and Lampert (1981), differences in survivorship of migrants due to fish predation offset a 2.5-fold reproductive advantage for nonmigrants.

Criticism of the visual predation hypothesis centers on several aspects, two of which are the presumed importance of fish predation and certain associated features of migrating organisms. For example, there is concern over the amplitude of vertical movement. Some question why particular prey species descend so deeply, presumably beyond the visual sensitivity of fish, while others question why plankters

seem to stop too shallow for concealment (McLaren 1963). Patterns of bioluminescence and pigmentation also seem to present additional problems. Why should migrants be luminous (McLaren 1963)? If transparency is an adaptation to visual predation, why should highly transparent forms migrate? Conversely, if predation is really as important as is presumed for freshwater ponds and lakes, why do so many large-bodied and heavily pigmented noncrustaceans co-occur with fish?

PHOTOPROTECTION HYPOTHESIS

There is a curious distribution of pigmentation in aquatic zooplankton. In freshwater pools and ponds, shallow-water or surface-film species are often highly pigmented, especially at high elevations and latitudes, while mid-water pelagic species are usually very transparent (Siebeck 1978a, Byron 1982, Hebert and McWalter 1983). Surface-dwelling marine species are also often pigmented, usually blue or violet, whereas pelagic species are often transparent and abyssal species are heavily pigmented—often red or black (Chapman 1976).

The advantage of maintaining pigmentation in shallow waters appears to be protection against harmful short-wave radiation, principally UV (Herring 1965, 1967). Low-level and short-duration exposures to UV radiation result in sunburn-like symptoms, reduce survivorship, and stimulate melanin production (Siebeck 1978a, 1978b). However, because UV radiation is absorbed rapidly in water, most pelagic species experience only limited doses, if any at all. The same cannot be said for slightly longer wavelengths of light, those that extend into the visible blue range. Blue wavelengths penetrate deepest in pure, clear waters. Recently Hairston (1976, 1978) expanded upon the work of Herring (1965, 1967), by proposing that carotenoid pigments serve a photoprotective role against blue-light damage to porphyrins, flavins, or quinones. Although there is some dispute over the original laboratory experiments (e.g., Ringelberg 1980b), avoidance of harmful short-wave radiation provides a viable alternative explanation for diel vertical migration (Huntsman 1924). Vertically migrating copepods suffer less mortality from sunlight than stationary populations, although even in relatively shallow waters, it is not clear whether the primary factor in migration is visual predation from fish or photoprotection (Byron 1982).

ASSOCIATED ADAPTATIONS

Transparency

Increased transparency in pelagic zooplankton is both a widespread and effective adaptation by aquatic organisms against visual predation. The resulting crypsis provides an evolutionary solution to the problem of concealment against a background that continually changes according to the predator's line of sight, the time of day, and the color of the water. Background colors are simply transmitted through the prey's tissues, thereby reducing contrast and producing an ideal camouflage. As an

adaptation, it is uniquely suited for an aquatic environment. Light that falls on an object can be absorbed, scattered, reflected, or transmitted. If there is a great disparity between the density of the organism and the surrounding medium—as is the case for terrestrial environments—light passing through an object would be refracted even if it were perfectly transmitted internally through tissues. The resulting refraction heightens brightness contrast with background colors and detracts from concealment. However, the density of living tissue and water is so close in an aquatic environment that refraction is minimized (except for gonadal tissue, which frequently contains lipids). Perhaps this simple feature, together with the photoprotective property of pigmentation, explains why transparency is so rare a predator-prey adaptation in terrestrial species, unless surfaces are relatively flat and removed from vital organs (e.g., transparent wings of Lepidoptera; Papageorgis 1975). Despite the frequent reference to transparency in aquatic studies of predator-prey interactions, this subject has received surprisingly little quantitative treatment. In freshwater ponds and lakes, several large-bodied types of zooplankton apparently survive exposure to fish through enhanced transparency (e.g., *Leptodora*, *Chaoborus*, certain helmeted *Daphnia*; see Zaret 1972, Zaret and Kerfoot 1975, O'Brien et al. 1979, Kerfoot 1980b).

The factors which influence survival and vertical migration of larval *Chaoborus*, the phantom midge, are especially well documented. In fishless pools and ponds, larval *Chaoborus* assemblages are dominated by large-bodied, translucent species that undergo limited vertical migration. When fish are present, the more visible species are eliminated and are replaced by moderate-sized species that undergo traditional diel vertical migration (Macan 1977; Northcote et al. 1978; Stenson 1978a, 1978b; von Ende 1979). In this migration, the fourth and third instars of the moderate-sized species move up from sediments or from lower strata to surface waters at sunset and then descend at sunrise (Northcote 1964, Goldspink and Scott 1971, Swift 1976). While oxygen concentrations modify patterns of emergence in very shallow or highly eutrophic waters (LaRow 1968, 1969, 1970), fish are known to selectively prey upon the fourth and third instars. Laboratory studies show that fish predation favors smaller-bodied species and those species that have reduced eye size and pigmentation (Stenson 1978a, 1978b, 1980). In mixed moderate-sized assemblages, smaller species undergo less vertical migration than relatively larger-bodied species, presumably reflecting the reduced risk associated with smaller size.

Few zooplankton cases are as well documented as the *Chaoborus* example, although transparency is a much more striking feature of the diverse marine community. In the so-called blue-water regions of the ocean, certain subgroups contain a high proportion of transparent species, e.g., the medusae, siphonophores, ctenophores, chaetognaths, pteropods, heteropods, appendicularians, salps, doliolids, pyrosomes, and many mesoplanktonic larvae (Hamner et al. 1975). To quote Chapman (1976)

Table 2

Transparency of selected marine and freshwater organisms, measured as percent transmittance of incident light in the visible range. All are whole-organism determinations unless otherwise noted.

Taxa	Percent Transmittance	Source
Marine:		
Dinoflagellata		
Noctiluca miliaris	0.90	Greze 1963
Hydromedusae		
Rathke octopunctata	0.80	Greze 1963
Polyorchis sp.	0.97*	Chapman 1976
Siphonophora		
Hippopodius hippopus	0.84	Greze 1963
Lencia sp.	0.86	Greze 1963
Scyphozoa		
Chrysoaora sp.	0.93*	Chapman 1976
Aurelia sp.	0.93*	Chapman 1976
Copepoda		
Pleuromemma gracilis	0.20	Greze 1963
Sapphirina metallina	0.16	Greze 1963
Corycaeus furcifer	0.43	Greze 1963
Pseudocalanus elongatus	0.55	Greze 1963
Haloptilus longicornis	0.90	Greze 1963
Copilia mediterranea	0.93	Greze 1963
Appendicularia		
Oikopleura dioica	0.85	Greze 1963
Freshwater:		
Cladocera		
Daphnia pulicaria	0.72	Kerfoot 1982
Daphnia rosea	0.72	Kerfoot unpublished
Bosmina longirostris	0.70	Kerfoot unpublished
Diaphanosoma brachyurum	0.81	Kerfoot unpublished
Leptodora kindtii	0.92	Kerfoot 1982
Copepoda		
Mesocyclops edax	0.58	Kerfoot unpublished
Insect		
Chaoborus flavicans	0.91	Kerfoot 1982
Chaoborus punctipennis	0.81	Kerfoot unpublished

* mesoglea

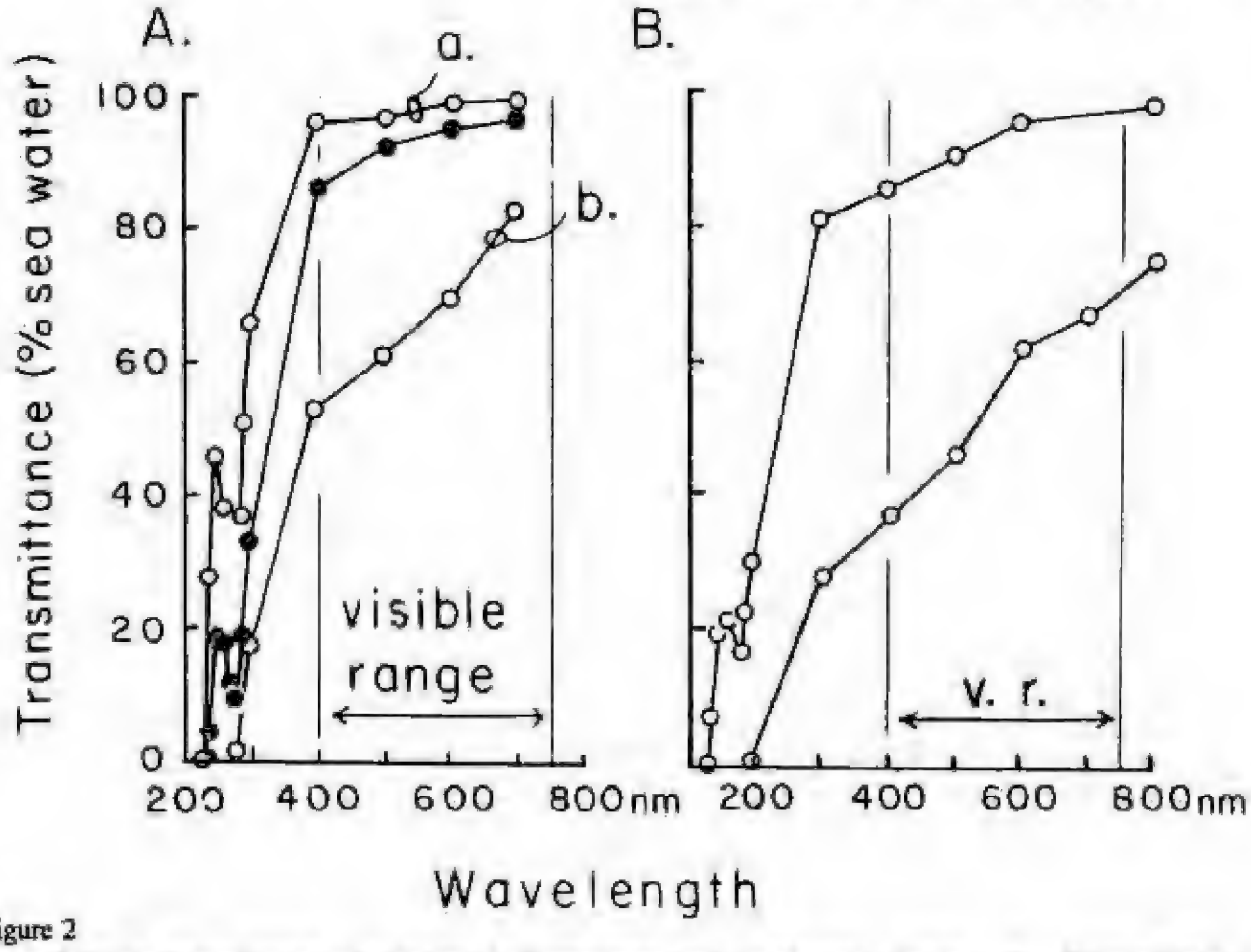

Figure 2

Relative transmittance of various hydromedusan and scyphozoan tissues. A. Transmittance of *Polyorchis* (hydromedusan) mesoglea (hollow dots), both as intact mesoglea (a) and as liquid expressed from mesoglea (b). Transmittance of *Chrysaora* (scyphozoan) mesoglea (solid dots). B. Transmittance of *Aurelia* (scyphozoan) mesoglea without (upper curve) and with (lower curve) subumbrella cell layer. In all cases, liquid or chunks cut to fit cuvette of a spectrophotometer. Redrawn from Chapman (1976).

> Where such animals are pigmented at all they are generally colored blue or violet, e.g., ***Rhizostoma***, ***Cyanea***, ***Velella***, ***Ianthina***, ***Clio***, ***Doliolum***, although there are exceptions to this such as ***Physophora***, ***Chrysaora***, and ***Beroe***. Other colorless or very lightly pigmented genera include ***Aurelia***, many hydromedusae, e.g., ***Polyorchis***, many siphonophores, e.g., ***Muggiaea***, ***Hippopodius***, ctenophores such as ***Pleurobrachia***, annelids such as ***Tomopteris***, the chaetognath ***Sagitta***, the crustaceans ***Cystosoma*** and ***Phronima***, the molluscs ***Carinaria*** and ***Gleba*** and the urochordates ***Salpa*** and ***Pyrosoma***. Needless to say, transparency is a matter of degree, but some species such as ***Sagitta*** and ***Tomopteris*** could be described as "glass-like."

Surprisingly few studies have attempted to quantify transparency (for exceptions, see Greze 1963, Chapman 1976, Kerfoot 1982). Table 2 summarizes transmittance values for several freshwater and marine organisms. For some of these species the degree of transparency is truly amazing. Well over 80–90% of incident light is transmitted through such varied body tissues as integument, connective tissue, digestive tract and muscle. Chapman's findings suggest that transmittance is often high at wavelengths beyond 400 nm, but declines rapidly for shorter wavelengths (Fig 2). Absorption of shorter wavelengths recalls the photodamage hypothesis, and raises the question of whether transparency might increase liability to shortwave radiation.

There is also the basic question of how inhomogeneous tissues become so transparent. Chapman (1976) considered four contributing properties: (1) colored or pigmented compounds must be absent; (2) many of the submicroscopic structures are considerably smaller than the shortest wavelength of visible light and are therefore relatively insignificant to scattering or refraction; (3) refractive index must be uniform as possible; and (4) destructive interference may reduce scattered light, allowing only directly transmitted rays to pass through tissue (applies to regularly arranged components, e.g., myosin filaments).

Although transparency is difficult to measure, the relative advantages of transparency are easily demonstrated in laboratory predator-prey experiments. With certain species of fish, the relative conspicuousness of two prey items can be quantified by measuring a "reactive distance" response (Confer and Blades 1975, Vinyard and O'Brien 1976). For example, prior to attack a centrarchid will reorient to face its prey and will extend its dorsal fin. This distinctive response of the predator to its prey allows an objective assessment of directed interest. This type of analysis can be very useful in encounter models. If two centrarchids (the pumpkinseed ***Lepomis gibbosus*** and the crappie ***Pomoxis annularis***) are presented with either ***Chaoborus*** or ***Daphnia***, the results are very similar (Fig 3). In each case, comparisons of reactive distance verify the importance of transparency in reducing conspicuousness of the midge larvae. Although much larger, ***Chaoborus*** stimulated no more interest than a moderate-sized ***Daphnia*** (Kerfoot 1982, Wright and O'Brien 1982). The extremely low reactive distances suggest that the fish are keying in on such small items as the pigmented eye or swim bladders (Wright and O'Brien 1982).

Despite reductions in reactive distance, highly transparent prey are still likely to migrate for two reasons. The first deals with postcapture experience, in particular the energetic reward to the predator and its effect on subsequent behavior. Because larger-bodied prey constitute a greater energetic prize for fish, occasional captures may only motivate a fish to search harder for a transparent prey (Ehlinger and Folt, personal communication). The second reason involves breakdown of the defense. Relatively small differences in refractive index between an object and the surrounding medium are emphasized when the object lies across a boundary between a bright and dark field. If fish align themselves so that they move along the edge of Snell's window, i.e., at an angle of $47-48^{\circ}$ with the vertical, the "dark field" effect will reveal even highly transparent prey (Lythgoe 1979, Janssen 1981). These reasons may explain why fish stomachs are often full of ***Chaoborus*** or ***Leptodora***, in spite of the high transparency of these prey species (e.g., Unger and Lewis 1983).

Bioluminescence

Recent work on predator-prey interactions has provided insights into two of the remaining areas of concern. On the question, why some vertically migrating organisms possess bioluminescent organs, Clarke (1963) suggested that the downward-directed photophores of marine fish and invertebrates serve as camouflage organs. That is, these organs could produce light that would match the color and

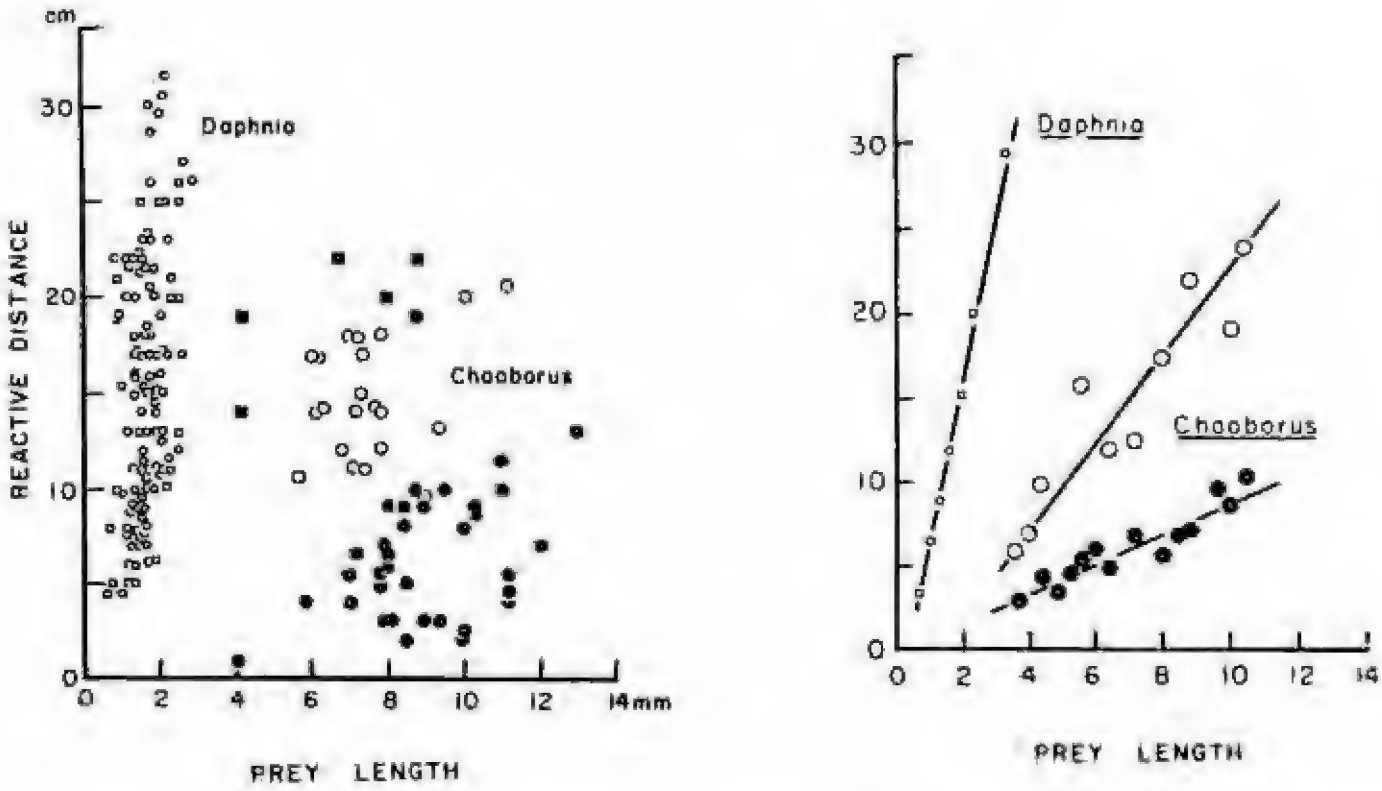

Figure 3

Reactive distance of pumpkinseeds (*Lepomis*) and white crappie (*Pomoxis*) to various sizes of *Chaoborus* and *Daphnia*. (A) Reactive distance of juvenile pumpkinseeds to *Daphnia pulicaria* (small circles), stationary (large solid dots) and moving (large hollow circles, solid squares) *Chaoborus*. Actual data points shown. (B) Reactive distance of small white crappie to *Chaoborus* sp. and *D. magna*. Solid dots are stationary *Chaoborus*, while large hollow circles are moving *Chaoborus*. Points are means of 3–30 observations. Figure A from Kerfoot (1982); figure B redrawn from Wright and O'Brien (1982)

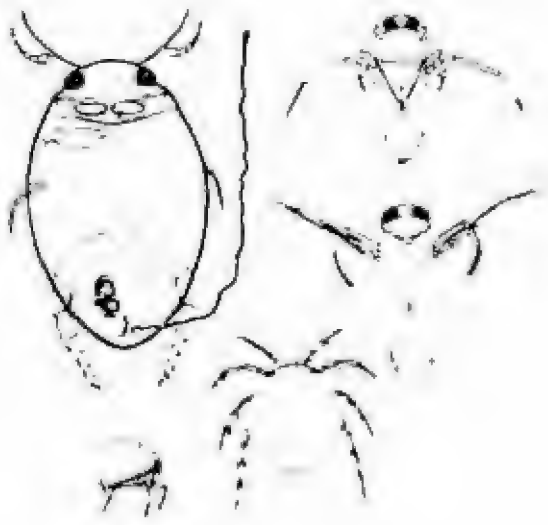

Figure 4

A few of the invertebrates that carry chemicals against fish. Clockwise from the upper left, these groups and their chemical substances include dytiscids (steroids from the prothoracic glands, acids from pygidial glands), corixids and notonectids (aldehydes), water mites (uncharacterized), and pleids (hydrogen peroxide).

radiance of downwelling daylight and would conceal the normally shaded ventral portion of the prey. Subsequent experiments, reviewed in Lythgoe (1979), confirm this idea and suggest widespread use of photophores for radiance matching and other predator-prey interactions. Thus the possession of bioluminescence is no longer an

argument against the predation hypothesis, but rather one now directly tied to it. The same can now be said for the co-occurrence of fish and many large-bodied, conspicuous invertebrates in ponds. Many of the more active noncrustacean taxa seem to employ chemical defenses against fish.

Chemical Defenses

The use of chemical defenses by aquatic organisms is probably much more widespread than commonly believed, involves a large number of species, and explains why many conspicuous organisms fail to avoid visual predators. Many species of bugs, beetles, water mites, tadpole larvae, and salamanders are actively rejected by fish in laboratory tests (Fig 4). In the case of water mites, exposure to fish selects for enhanced unpalatability and aposematism (Kerfoot 1982). Often noxious chemical substances are secreted over the body surface or voided on contact (Kerfoot 1982, Kerfoot and Scrimshaw, unpublished observations). Identified compounds include acids, aldehydes, esters, and even "vertebrate" steroids (Table 3). Preliminary assays suggest that the unusual nature of some of these compounds (i.e., different from the traditional secondary chemical defenses of terrestrial arthropods) stems from: (1) effectiveness in an aquatic medium (Hepburn et al. 1973) and (2) the nature of the primary target, i.e., directed against cold-blooded vertebrates (fishes), rather than exclusively against arthropods or warm-blooded vertebrates.

SUMMARY AND CONCLUSIONS

In recent years interest in vertical migration seems to have increased, inspired by preliminary tests of alternative hypotheses. In terms of providing a reason why grazers descend at dawn and rise again at dusk, the energetic/metabolic arguments appear seriously weakened by overall temperature effects. When demographics are framed in a realistic and comprehensive manner, the energetic/metabolic arguments neglect the influence of temperature on egg development and maturation. While there may be a slight metabolic advantage to resting in cooler waters during half the day, temperature differences between upper and lower strata require a major increase in fecundity to compensate for developmental delays. Moreover, residence in cool waters may actually increase mortality if mortality is presumed time-dependent (Ohman et al. 1983). Finally, since migrating individuals usually move away from their primary food source, reproduction is much lower for these individuals (see data in Stich and Lampert 1981).

In contrast, the predation and photodamage hypotheses provide reasonable, straightforward reasons why zooplankton should descend at dawn and rise again at dusk. However, the predation hypothesis is somewhat incomplete as originally formulated, since it dealt only with differential survivorship. A more comprehensive perspective should address demographic tradeoffs, i.e., evaluate the gain in fecundity associated with remaining close to food versus the risk from visual predators. Field examples of this approach are the preliminary studies of Stich and Lampert (1981)

Table 3

The chemical defenses of various pond organisms. Information includes the taxon, number of species from which compounds isolated, published description of glands which manufacture and void substance (+ , name), and chemicals. Most of references from Blum (1981) and Dettner (1979); water mite information in Kerfoot (1982).

Taxon	Number of Species	Glands	Chemical Compounds
Insecta			
Hemiptera (Bugs)			
Notonectidae (Backswimmers)			
Notonecta	1	+	p-hydroxybenzaldehyde p-hydroxybenzoic acid
Corixidae (Water Boatmen)			
Corixa	1	+	trans-4-oxo-hex-2-enal
Sigari	1	+	trans-4-oxo-hex-2-enal
Pleidae (Pigmy Backswimmers)			
Plea	1	0	hydrogen peroxide
Coleoptera (Beetles)			
Dytiscidae (Predacious Diving Beetles)			
Dytiscinae	13	+	Prothoracic glands with steroids
Colylmbetinae	25	+	9 identified pregnene derivatives,
Hydroporinae	17	+	8 pregnediene derivatives, 3 non-steroids. Pydidial glands with 16 identified compounds, including acids, esters, and hydorquinone
Gyrinidae(Whirligig Beetles)			
Dineutes	5	+	Pygidial glands with
Gyrinus	5	+	4 major compounds: gyrinidal, isogyrinidal gyrinidione, and gyrinidone
Arachnoidea			
Hydracarina (Water Mites			
Limnochares	16	+	Almost all water mites
Eylais			posses numerous skin
Hydrachna			glands (glandularia).
Piona			Compounds uncharacterized
Limnesia			
Neumania			
Diplodontus			
Arrenurus			

and Ohman et al. (1983), which suggest a 50−250% advantage for prey that move away from vertebrate or invertebrate predators. In the future, studies should concentrate on certain weak areas: (1) accurate assessment of predator density, size structure, and feeding habits, in order to directly or at least indirectly assess the potential importance of predation; (2) detailed studies of prey food limitation at the intraspecific, interspecific and community levels; and (3) direct exclosure/enclosure tests of alternative hypotheses.

The blue-light photodamage hypothesis provides an exciting revival of an old theme and an alternative reason for diel vertical migration. However, chief concerns center on light transmission through the water column and on the protective role of pigments. While UV radiation has been shown to produce harmful effects in surface-dwelling organisms and in shallow-water environments, the association between blue wavelengths and carotenoid pigmentation is less convincing and requires further research. Studies should be directed at evaluating the influence of short-wave radiation on zooplankton behavior, physiology and survivorship, concentrating on those wavelengths that penetrate deepest in the water column.

An intriguing connection between the visual predation and photoprotection hypotheses lies in prey pigmentation. Enhanced transparency might increase susceptibility to photodamage. Yet resolution of the tie and its relationship to vertical migration are complicated by fortuitous side-effects. Migration to avoid visual predation automatically reduces exposure to daytime shortwave radiance. These drawbacks can be overcome, however, by judicious use of clones (e.g., in *Daphnia*) and by an enclosure design that allows independent manipulation of wavelengths and fish.

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COMPARATIVE MECHANISMS OF ALGAL MOVEMENT IN RELATION TO PHYTOPLANKTON PRODUCTION

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ABSTRACT

Some physiological mechanisms which enable different groups of algae to undergo depth regulation in lakes and oceans are considered. These include buoyancy control in blue-green algae by means of intracellular gas vacuoles, "swimming" by flagellates and possible mechanisms for varying sinking rates, especially for apparently nonmotile species. The main factors affecting active movements of phytoplankton—light, temperature and nutrient availability—are compared for different means of locomotion. Rates of movement are considered in relation to scales of time and space. Examples from an English lake are used to illustrate how behavioral responses of particular species or algal groups may influence their production both seasonally and through time.

INTRODUCTION

In this paper algal migrations are defined as the movement of cells under physiological control into different habitats according to season, climate and nutrient availability. Accumulations of algae in the surface layers of natural waters as a result of active movements have been observed since earliest times. The biblical plague in which the river turned to blood (*Exodus*, Chapter 7) has often been attributed to an algal bloom. More recently, the conspicuous and often sudden appearance of dense masses of phytoplankton in surface waters as "water-blooms" of blue-green algae (Cyanophyta) (e.g., Reynolds and Walsby 1975) and "red tides" due to dinoflagellates (Pyrrophyceae) (e.g., Eppley, Holm-Hansen and Strickland 1968; Berman and Rodhe 1971; Cullen, Horrigan, Huntley and Reid 1982) have been intensively studied. These phenomena normally result from upward movements frequently coupled with physical aggregation and lateral transport by water movements. Besides movements into the surface layers, many phytoplankton undergo depth regulation to form maxima at intermediate depths, and some may move in and out of the sediments.

The physiological mechanisms whereby different algae may exert control over their vertical position in the water column have been the subject of many specialist studies. Buoyancy regulation mechanisms are common to both marine and freshwater phytoplankton and are considered briefly here. They are compared in relation to scales of time and space together with the main factors, other than turbulence and advection, that influence algal movements. Examples from an English lake are used to illustrate how different behavioral responses of particular species or algal groups may interact with physical and chemical factors to influence phytoplankton production, both seasonally and over periods of years.

PHYSICAL CONSIDERATIONS

The physical forces affecting the movement of algal cells may be considered as those that control the movement of inert particles suspended in a viscous medium relative to the cells. The hydrodynamics of sinking and floating phytoplankton has been discussed in detail (e.g., Hutchinson 1967 and Walsby and Reynolds 1980) as has the subject of water movements (e.g., Mortimer 1974). Because of these lucid accounts only two of the principal considerations are described here.

For most phytoplankton which sink or float, water moves past in laminar flow (Walsby and Reynolds 1980). Under such conditions the terminal sinking velocity of cells or colonies, v, is given by the Stokes' equation for nonspherical particles, i.e.,

$$v = \frac{2}{9} g r^2 (\rho_1 - \rho) \eta^{-1} \phi_r^{-1} \qquad (1)$$

where g is the acceleration due to gravity, η the coefficient of viscosity of the suspending medium of density ρ, ρ_1 the density of the cells or colonies of radius r, and ϕ the "coefficient of form resistance" which is the ratio of the velocity of an equivalent sphere to that of cells of similar density and volume.

Phytoplankton may only regulate their depth when their rates of vertical movement exceed that of the surrounding medium. Natural waters are seldom motionless, due to the effects of wind and convectional mixing. The degree of turbulence is determined by the intensity of vertical density gradients and the work required to overcome them. The point at which turbulence overcomes stable horizontal flow may be quantified by the nondimensional ratio (density gradient)/(shear)^2, or Richardson number, i.e.,

$$Ri = \frac{g \frac{\partial \rho}{\partial z}}{\bar{\rho} \left(\frac{\partial u}{\partial z} \right)^2} \qquad (2)$$

where g is the acceleration due to gravity, ρ the density of water, $\bar{\rho}$ is the average density of water over the relevant depth interval, u the mean horizontal water velocity, and z the depth. Only below a critical value of 0.25 for Ri do turbulence and mixing overcome stable horizontal flow; for values between 0.5 and 1.0 the water is sufficiently stable for depth regulation by phytoplankton to become possible (Ganf 1974). Density gradients are often determined in phytoplankton studies, but current

velocities, which would allow calculation of values of ***Ri***, are rarely measured (e.g., Ganf 1974; Heaney and Talling 1980a; Cullen, Stewart, Renger, Eppley and Winant 1983). Greater reliance is usually placed on intuitive or empirical assessment of temperature or density gradients for determining water stability.

ALGAL MOVEMENTS

Blue-green Algae

The principal mechanism of buoyancy control in most planktonic blue-green algae, is by the regulation of gas vacuoles. Klebahn (1895) noticed that when sufficient pressure was applied to gas vacuoles in blue-green algae, then the gas vacuoles disappeared and the algae sank. This early observation was subsequently investigated by Walsby (1971) who quantified the pressure relationships of gas vacuoles and provided the theory and experimental evidence for gas vacuole regulation and buoyancy control (for reviews see Walsby 1972, Reynolds and Walsby 1975).

Gas vacuoles are aggregates of vesicles with gas-permeable, proteinaceous walls which may be collapsed by the application of pressure. In natural waters the pressure exerted on these vesicles is the sum of atmospheric pressure, hydrostatic pressure due to depth, cell turgor pressure at the vesicle wall, and pressure from surface tension at the cell wall and vesicle wall. When these combined pressures are greater than a certain critical pressure, the gas vacuole will collapse. Whether a gas vacuolate blue-green alga sinks or floats will depend on its density relative to the suspending medium. The cell density will depend upon its relative gas vacuolation and other density changes due to changing proportions of major cell constituents of different densities such as protein, carbohydrate, lipid and polyphosphate. These components of cell density are dependent upon a number of factors including growth rate, the relative flux of nutrients to the cells (especially carbon and nitrogen), light and the depth of suspension of the cells.

It has been shown for freshwater blue-green algae that buoyancy regulation due to changes of relative gas vacuolation enables a variety of behavioral responses rom (1) diel vertical migrations, e.g., ***Microcystis aeruginosa*** Kütz and ***M. flos-aquae*** (Wittr.) Kirchn. in tropical Lake George, Uganda (Ganf 1974) and ***Aphanizomenon flos-aquae*** (Konopka, Brock and Walsby 1978); (2) the formation of relatively stable layers in the metalimnion of some lakes, e.g., ***Oscillatoria agardhii***, var. ***isothrix***, Skuja (e.g., Lund 1959, Walsby and Klemer 1974) and (3) seasonal migrations of meroplanktonic forms to and from the sediments, e.g., ***M. aeruginosa*** (Preston, Stewart and Reynolds 1980). The marine genus ***Trichodesmium*** contains species with gas vacuoles whose vesicles are much stronger than in freshwater forms. Walsby (1978) considers this increased strength an adaptation to the greater hydrostatic pressure at the depths to which the organisms occur.

Most effort has been concentrated on the study of gas vacuolation as the major means of buoyancy control. However, attention is now being turned to the fine-tuning of cell density due to changing proportions of cell constituents mentioned above (Oliver, Utkilen and Walsby 1983) and decreasing cell density by increasing cell

mucilage (Walsby and Reynolds 1980).

Diatoms

There is an increasing awareness and interest in the manner by which diatoms can regulate their sinking rate under stable water conditions. A common feature of many planktonic diatoms is that senescent cells sink 2−7 times more rapidly than actively growing ones (e.g., Smayda and Boleyn 1965, 1966a, b; Titman and Kilham 1976; Wiseman and Reynolds 1981). Nutrient depletion by the major nutrients, carbon dioxide and silicon, causes an increase in sinking rate, whereas there is a variable response to nitrogen and phosphorus depletion with increased sinking rate in some species but decreased in others (Bienfang, Harrison and Quarmby 1982). Three discrete levels of sinking rate have been recognized by Eppley, Holmes and Strickland (1967) for marine diatoms: (a) neutrally buoyant cells, (b) exponentially growing cells which sink, and (c) nongrowing cells which sink more rapidly. As changes of sinking rate occur quite rapidly and are reversible, they are generally regarded as being physiologically controlled. The physical variables controlling diatom sinking are given in Stokes equation (1). Of these r, the effective cell or colony radius, is mathematically the most sensitive variable as it is a squared function, but there is little evidence of change in r with variable sinking rate.

Some marine diatoms may alter their density by regulation of the ionic composition of the cell sap. Anderson and Sweeney (1978) have shown that cells of ***Ditylum brightwellii*** (West) Grun. may increase their density by accumulating K^+ and losing Na^+ from the vacuoles and that such changes of density were sufficient to account for observed diel changes of sinking rate. It would seem unlikely that this is the sole means of density and sinking rate regulation in marine diatoms, and ionic regulation of density is improbable in freshwater of low ionic strength.

The freshwater diatom ***Asterionella formosa*** Hass. sinks more rapidly under conditions of phosphorus depletion and senescence (Titman and Kilham 1976) and CO_2 depletion (Jaworski, Talling and Heaney 1981). Sufficient changes of density to account for observed changes in sinking rate were not found by Wiseman, Jaworski and Reynolds (1983). Neither were they able to determine changes in the electrophoretic mobility of the cells with variable sinking rate. This would have supported the hypothesis that surface charge effects can alter the viscosity of the medium which surrounds the algal cells (Wiseman and Reynolds 1981). The physiological mechanism controlling sinking rate in freshwater diatoms remains unknown and a challenge for future work.

Flagellates

Unlike the two previous groups, flagellates possess an effective and responsive means of propulsion. This gives enhanced ability for precise depth regulation enabling the algae to obtain optimum optical depth, migrate into nutrient-rich layers and avoid detrimental conditions.

As with blue-green algae, flagellates show a spectrum of behavioral movements. They may undertake appreciable diel vertical migrations, e.g., ***Gonyaulax polyedra***, ***Prorocentrum micans***, ***Ceratium fusus***, ***C. tripos*** (Hasle 1950), and ***C. hirundinella*** (O.F. Müll.) Bergh (Talling 1971), form apparently stationary midwater layers, e.g., ***C. hirundinella*** (Heaney and Talling 1980a), and form cysts migrating seasonally to and from the benthos, e.g., ***Gonyaulax tamarensis*** (Anderson and Morel 1979) and ***C. hirundinella*** (Heaney, Chapman and Morison 1983).

Planktonic flagellates are mainly phototactic and regulate their vertical position during daytime in response to the underwater light climate. Although this response may be modified by the physiological and nutrient status of the cells, perhaps through geotaxis, it would appear that different species have preferred optical depths. In Lake Constance two closely related species of ***Rhodomonas*** undergo simultaneous diel vertical migrations, but from sunrise until afternoon they adjust their vertical position at different depths and irradiances (Sommer 1982). When both species were incubated in situ at different depths, there was a vertical niche separation for growth in accordance with their vertical distribution (Heaney and Sommer 1984).

Flagellates are reported to undergo diel vertical migrations, descending into deep, nutrient-rich layers at night and moving into the euphotic zone during day, and so acting as a "nutrient pump" (e.g., Eppley et al. 1968). Such behavior has been demonstrated experimentally using cultures in laboratory columns (Heaney and Eppley 1981, Cullen and Horrigan 1981).

There are several observations of migrations in darkness which are not regulated by phototaxis (e.g., Eppley et al. 1968, Heaney and Furnass 1980, Cullen and Horrigan 1981). Although circadian rhythms of migrations may be important, Eppley et al. (1968) postulated a geotactical response governed by a rhythmic shift of organelles within the cells which thus altered the center of gravity. Chapman, Livingstone and Dodge (1981) suggested that excysting cells of ***Ceratium hirundinella*** on the benthos are able to orient by geotaxis and thus swim into the illuminated upper zone due to the asymmetric deposition of lipid and carbohydrate into the anterior and posterior of the cell (Fig 1).

Rates of Movement

There is a wide range of vertical velocities for algal species from a few centimeters per day to almost 100 m per day (Table 1). Swimming speeds for vertically migrating flagellates of approximately 1−2 m per hour have been recorded (e.g., Hasle 1950, Eppley et al. 1968).

Production by phytoplankton depends upon maintenance of cells within the euphotic zone by turbulent mixing, active movements or both. The depth of the euphotic zone may be barely a meter in shallow productive lakes to over a hundred meters in deep oligotrophic waters. Although it may seem advantageous to have large species with high rates of movement in the latter situation, paradoxically, the opposite is generally the case. Small species comprise most of the phytoplankton in oligotrophic lakes (e.g., Wetzel 1983, p. 362) and oceans (Bienfang, Szyper and Laws 1983) and are probably favored because nutrient uptake is enhanced as a result of large ratios of surface area to volume. Moreover, because of the large vertical distance involved and the low rates of movement of the cells, Bienfang, Harrison and Quarmby (1982) considered that rapid change of water around the cells is more significant than downward movement into nutrient rich layers for nutrient uptake. Larger species are more characteristic of productive waters with shallow mixed layers where rapid depth regulation in steep gradients of light and nutrients may be more important.

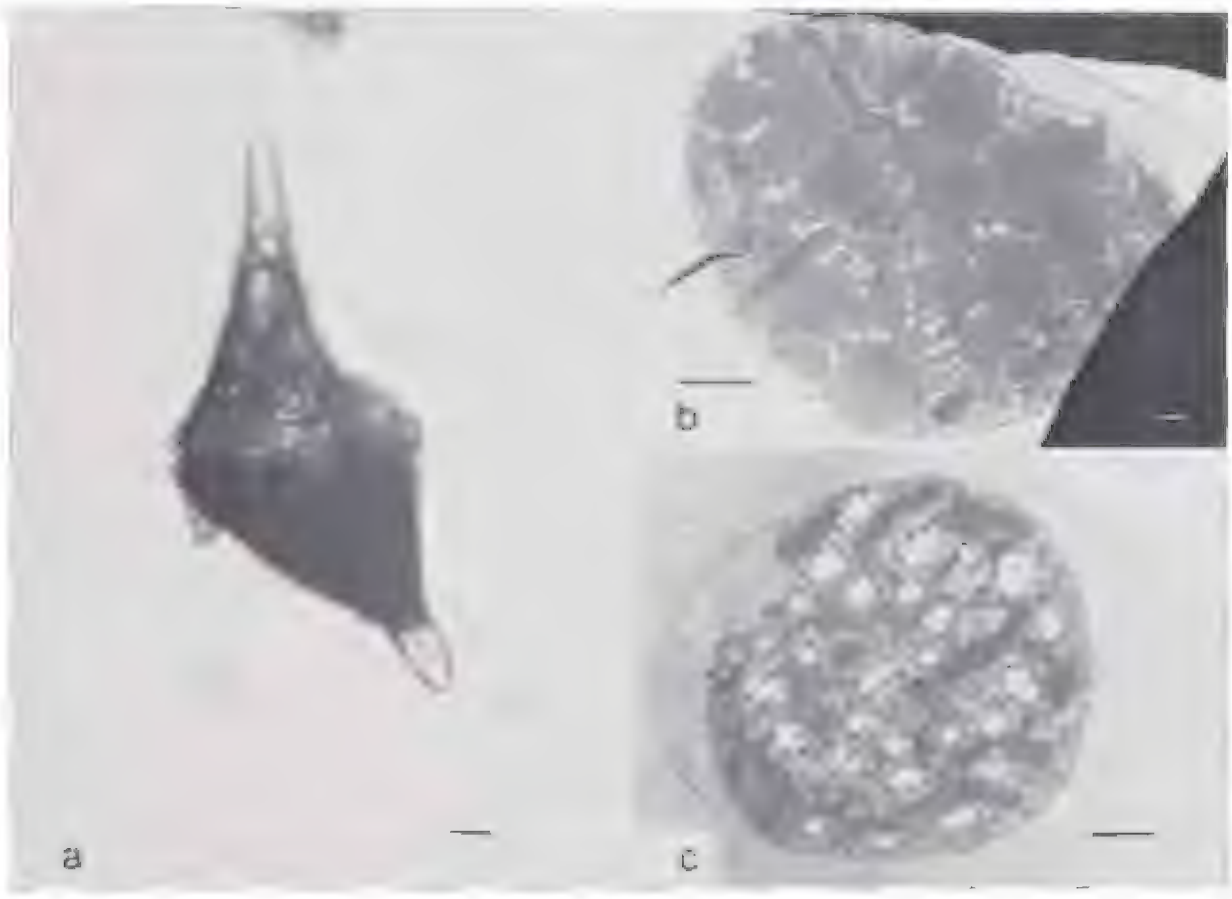

Figure 1

Polarization of carbohydrate and lipid reserves in preceratium stage of ***Ceratium hirundinella***: (a) light photomicrograph of cell stained with Lugol's iodine showing deposition of carbohydrate in the posterior region; (b) and (c) transmission electron micrographs of sections cut through the anterior and posterior regions of a cell showing the distinct segregation of lipid and carbohydrate respectively. Bar ≈5μm (b and c courtesy Dr. D.V. Chapman).

Table 1

Rates of vertical movements measured for natural and cultured populations of diatoms and blue-green algae; NP = natural populations, C = cultures, E = exponential phase, S = stationary phase, −Si = silicon depleted, −N = nitrogen depleted, −P = phosphorous depleted, $-CO_2 = CO_2$ depleted, ↓ = sinking, ↑ = floating, +GV = with gas vacuoles, −GV = without gas vacuoles.

Species		Sinking or Floating Rate $m \cdot day^{-1}$	Temperature °C	References
Marine Diatoms				
Skeletenoma costatum	E,C	0.025 ↓	16	1
(Grev.) Cleve	−Si,C	0.50 ↓	16	1
	−N,C	0.06 ↓	16	1
	−P,C	0.19 ↓	16	1
	E,C	0.30 ↓	15	2
	S,C	1.35 ↓	15	2
Chaetoceros gracile	E,C	0.15 ↓	16	1
Schütt	−Si,C	0.80 ↓	16	1
	−N,C	0.15 ↓	16	1
	−P,C	0.12 ↓	16	1
Chaetoceros didymus	E	0.23 ↓	20	3
Chaetoceros lauderi	E,C	0.46 ↓	15	4
Ralfs	S,C	1.54 ↓	15	4
Ditylum brightwelli	E,C	0.40 ↓	16	1
(West) Grun.	−Si,C	2.00 ↓	16	1
	−N,C	0.07 ↓	16	1
	−P,C	0.25 ↓	16	1
	E,C	1.1−1.4 ↓	20	5
Coscinodiscus wailesii	E,C	0.25 ↓	16	1
(Gran et Angst)	−Si,C	2.30 ↓	16	1
	−N,C	0.90 ↓	16	1
	−P,C	2.60 ↓	16	1
Thalassiosira weissflogii				
(Grunow) Fryxell and Hasle				
low light ($< 28\ \mu \cdot E \cdot m^{-2} \cdot s^{-1}$)	E,C	0.10 ↓	–	6
high light ($> 64\ \mu \cdot E \cdot m^{-2} \cdot s^{-1}$)	E,C	0.23 ↓	–	6
Thalassiosira cf. *nana*	E,C	0.10 ↓	15	7
Lohmann	S,C	0.28 ↓	15	7
Thalassiosira rotula	E,C	0.41 ↓	15	7
Meunier	S,C	2.10 ↓	15	7
Rhizosolenia setigera	E,C	0.16 ↓	15	2
Brightwell	S,C	1.77 ↓	15	2

Table 1 (continued)

Species		Sinking or Floating Rate m ·day $^{-1}$	Temperature °C	Reference
Bacteriastrum hyalinum	E,C	0.39 ↓	15	4
Lauder	S,C	1.27 ↓	15	4
Nitzschia seriata	E,C	0.26 ↓	15	7
Cleve	S,C	0.50 ↓	15	7
Freshwater Diatoms				
Fragilaria crotonensis	NP	0.2–0.65 ↓	–	8
Kitton	C	0.2–0.80 ↓	–	8
Melosira italica subsp. ***subartica*** O. Müll	NP	1.00 ↓	0	9
Melosira agassizii	E,C	0.67 ↓	–	10
	S,C	1.87 ↓	–	10
Cyclotella meneghiniana	E,C	0.08 ↓	–	10
	S,C	0.24 ↓	–	10
Asterionella formosa	E,C	0.20 ↓	–	10
Hass.	S,C	1.48 ↓	–	10
	–P,C	0.50 ↓	–	10
	E,C	0.25 ↓	20	11
	$-CO_2$,C	1.00 ↓	20	11
	E,C	0.20 ↓	10	12
	S,C	1.00 ↓	10	12
	NP	0.12–0.32 ↓	0	9
Freshwater Blue-green Algae				
Microcystis aeruginosa	NP	1.00–1.50 ↓	–	13
Kutz emend. Elenkin	NP	0.30–1.50 ↑	–	13
	NP	9.20 ↑	–	15
Microcystis aeruginosa Kutz	NP	92 ↑	25	16
Oscillatoria agardhii var ***isothrix***	NP	0.07–0.70 ↓	–	13
Skuja	NP	0.14–0.30 ↑	–	13
Oscillatoria agardhii var ***isothrix***	NP	0.04 ↑	–	14
Aphanizomenon flos-aquae Ralfs ex Born. et Flah.	NP	1.40 ↑	–	15

Table 1 (continued)

Species		Sinking or Floating Rate m ·day $^{-1}$	Temperature °C	Reference
Anabaena spiroides				
f. *spiroides*	NP	2.60 ↑	–	15
Kleb.				
Anabaena circinalis	NP	5.12 ↑	–	15
Rabenh. ex Born. et Flah.				
Coelosphaerium naegelianum	NP	3.60 ↑	–	15
Unger				
Oscillatoria agardhii	NP,+GV	0.40 ↑	–	17
Gom.	NP,−GV	< 0.10 ↓	–	17
Oscillatoria redekei	C,+GV	0.030 ↑	20	18
Van Goor	C,−GV	0.025 ↓	20	18
Marine Blue-green Algae				
Trichodesmium erythraeum	NP,+GV	0.20 ↑	–	19
Ehrenberg	NP,−GV	0.18 ↓	–	19
Trichodesmium thiebautii	NP,+GV	0.06 ↑	–	19
Gomont	NP,−GV	0.10 ↓	–	19
Trichodesmium contortum	NP,+GV	0.04 ↑	–	19
Wille	NP,−GV	0.07 ↓	–	19

References: (1) Bienfang, Harrison and Quarmby (1982); (2) Smayda and Boleyn (1966a); (3) Eppley, Holmes and Strickland (1967); (4) Smayda and Boleyn (1966b); (5) Anderson and Sweeney (1977); (6) Bienfang, Szyper and Laws (1983); (7) Smayda and Boleyn (1965); (8) Reynolds (1976); (9) Lund (1959); (10) Titman and Kilham (1976); (11) Jaworski, Talling and Heaney (1981); (12) Wiseman and Reynolds (1981); (13) Reynolds (1978); (14) Walsby and Klemer (1974); (15) Reynolds and Walsby (1975); (16) Ganf (1974); (17) Walsby, Utkilen and Johnsen (1983); (18) Gibson (1975); (19) Walsby (1978).

FACTORS AFFECTING ALGAL MOVEMENTS

The disposition of phytoplankton is governed by the interaction of external, internal and species-specific factors. The most important external factors are turbulent mixing and gradients of light, temperature, and nutrients. Under stable conditions it is the relative flux of energy and the major nutrients in relation to cell need which often lead to changes in behavior. Phytoplankton are often observed to aggregate at depths conducive to growth or maintenance, although occasionally populations become stranded in adverse conditions as with surface blooms of blue-green algae under high irradiance. The theoretical framework for factor interaction along intersecting vertical gradients for phytoplankton photosynthesis has been discussed by Talling (1979).

Table 2

Factors influencing the vertical orientation and rates of movement of diatoms and blue-green algae where S = sinking rate, B = bouyancy, + = increased, − = decreased. Flagellates tend to move to preferred optical depths during daytime and C+ and C− indicate constrained upward or downward movements respectively. The references give only recent examples.

	Factor	Response	Reference
Diatoms	High irradiance	+S	1
	Low irradiance	−S	1
	High temperature	+S	2
	Si-depletion	+S	3
	P-depletion	−S	3
		+S	3,4
	N-depletion	−S	3
		+S	3
	CO_2-depletion	+s	5
	senescence	+S	6
Blue-green	High irradiance		
Algae (gas	(Increased turgor pressure)	−B	7
vacuolate)	Low irradiance		
	(Decreased turgor pressure)	+B	7
N-depletion	(Decreased RGV†)	−B	8
	CO_2-depletion		
	(Increased RGV)	+B	9
	P-depletion	−B	9
	Increased depth		
	(Increased hydrostatic		
	Pressure)	−B	10,11
Flagellates	High irradiance	none	12,13
		C+	14,15,16
	N-depletion	C+	12,13,17
	P-depletion	C+	12
	Temperature gradient	none	13
		C−	15,18
	Anoxic water	C−	19

† RGV = Relative gas vacuolation

(1) Bienfang, Szyper and Laws (1983); (2) Bienfang and Szyper (1982); (3) Bienfang, Harrison and Quarmby (1982); (4) Titman and Kilham (1976); (5) Jaworski, Heaney and Talling (1981); (6) Wiseman and Reynolds (1981); (7) Walsby (1971); (8) Klemer, Feuillade and Feulillade (1982); (9) Booker and Walsby (1981); (10) Reynolds (1973); (11) Walsby (1978); (12) Heaney and Eppley (1981); (13) Cullen and Horrigan (1981); (14) Heaney and Talling (1980); (15) Heaney and Furnass (1980); (16) Sommer (1982); (17) Eppley, Holm-Hansen and Strickland (1968); (18) Kamykowski (1981); (19) George and Heaney (1978).

As a result of the many studies of depth regulation by phytoplankton both in nature and in experimental enclosures, some generalizations may be made regarding vertical movement in different groups (Table 2). Even acknowledging factor interactions and the nuances of behavior of particular species, there are some marked differences between groups which play an important role in determining their production. For example, diatoms are essentially destined to sink, unlike blue-green algae and flagellates which may move up or down. Thus at least an intermittent turbulence is necessary for maintaining diatoms within the euphotic zone, whereas Pollinger and Zemel (1981) have shown that turbulence inhibits cell division in the dinoflagellate ***Peridinium cinctum*** forma ***Westii*** (Lemm.) Lefévre.

Of particular interest is the effect of CO_2 depletion which can occur in productive, soft-water lakes (Talling 1976). CO_2-depleted diatoms cease growing and sink more quickly than exponential phase cells (Jaworski et al. 1981), whereas carbon depletion in blue-green algae (which usually occurs at a relatively high pH due to the ability of these cells to utilize bicarbonate ion (Talling 1976)) results in increased buoyancy through inhibition of photosynthesis and cell turgor pressure regulation (Booker and Walsby 1981; Klemer, Feuillade and Feuillade 1982). The same factor may therefore cause the opposite response in different groups in a complex manner.

BEHAVIOR AND PRODUCTION

The significance of algal behavior in production ecology of phytoplankton communities is of growing interest. Species rarely exist in complete isolation from one another for long periods of time but coexist in a dynamic and changing environment. Production by one species or group depends upon adequate light and nutrients, the availability of which may be controlled or influenced by the presence of populations of other species. The remainder of this work concerns seasonal and long-term production of diatoms, dinoflagellates and blue-green algae in Esthwaite Water, a small productive English lake. For nearly forty years the phytoplankton of this lake has been regularly enumerated and the physiological ecology of the major species has been studied. This work has provided valuable information concerning the interrelationships and population dynamics of algal groups with different behaviors. Physical, chemical and biological field data presented here were obtained according to the methods described by Heaney and Talling (1980a) and Mackereth, Heron and Talling (1978).

Asterionella formosa has usually dominated the vernal algal maximum since the first regular counts of Dr. J.W.G. Lund in 1945 until the present day. However, with enrichment of the lake in the 1960's the summer biomass has increased due to the large populations of the dinoflagellate ***Ceratium hirundinella***, mainly at the expense of blue-green algae (Lund 1981). In some summers the preeminence of ***Ceratium*** has been such that only very small quantities of other species were present (e.g., Heaney and Talling 1980a). Nevertheless, there have been years during the period of ***Ceratium*** dominance when appreciable populations of diatoms and blue-green algae have occurred during stratification, showing that their growth is possible, given suitable conditions.

Growth Rates

Growth rates of unialgal cultures of three important species of algae, the dinoflagellate ***Ceratium hirundinella***,[1] the blue-green alga ***Oscillatoria bourrellyi***, and the diatom ***Asterionella formosa***, in the plankton of English Lakes, Esthwaite Water and Windermere, are shown in Figure 2. Cultures were grown in solution 10 of Chu (1942) as modified by Butterwick, Heaney and Talling (1982) at 20 ± 2°C and under a 12:12 hour light : dark cycle. Illumination was provided by daylight fluorescent lamps. Irradiance values (400−700 nm, photosynthetically available radiation, calculated in terms of $\mu Em^{-2} \cdot s^{-1}$) were measured with a scalar quantum sensor (Biospherical Instruments Inc., model QSP 200) submersed in growth medium inside the culture vessels. Biomass was determined using the inverted microscope technique to obtain cell counts or by attenuance measurements at 680 nm for ***Oscillatoria***. At 20°C ***Ceratium*** grow more slowly and with a higher onset of light saturation for growth than the other two species. There was no marked inhibition of growth at high irradiances except for ***Asterionella***, but even then its growth remained fastest of the algae studied. At low temperatures (< 10°C), both ***Ceratium*** (Heaney et al. 1983) and ***Oscillatoria*** (Heaney, unpublished) grow very slowly, and their growth season is accordingly severely restricted. By contrast, ***Asterionella*** grows relatively quickly at temperatures between 4° and 20°C (Talling, 1955) enabling it, on temperature grounds alone, to achieve rapid growth throughout the year.

The frequent summer dominance of ***Ceratium*** in Esthwaite Water clearly does not depend on a higher maximum growth rate than other species. Its success depends upon a number of factors discussed by Heaney and Talling (1980b). These include (a) recruitment of the inoculum from overwintering cysts in the sediment, (b) negligible grazing by zooplankton due to its large size, (c) relative freedom from parasitic fungal attacks on the vegetative cell, (d) high mobility for positioning at preferred optical depths during day and vertical migrations into deeper (nutrient rich) layers at night, and (e) a low coefficient of self-shading (increment of vertical extinction coefficient of light per unit chlorophyll ***a***, as ln units $\cdot mg \cdot m^{-2}$) permitting a higher upper limit of chlorophyll ***a***, in unit area of the euphotic zone (Talling 1971). The last characteristic may enable ***Ceratium*** to utilize more effectively the available nutrients and obtain a greater biomass before becoming light-limited through self-shading.

Of as great importance for summer phytoplankton production are the factors which perturb the usual slow but steady growth of ***Ceratium*** and enable other species to grow. Of these the most obvious is the severity of the weather and its effect on the stability of stratification.

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1. There is some uncertainty as to the correct taxonomic position of this alga which has some characteristics of *C. **furcoides*** (Levander) Langhans.

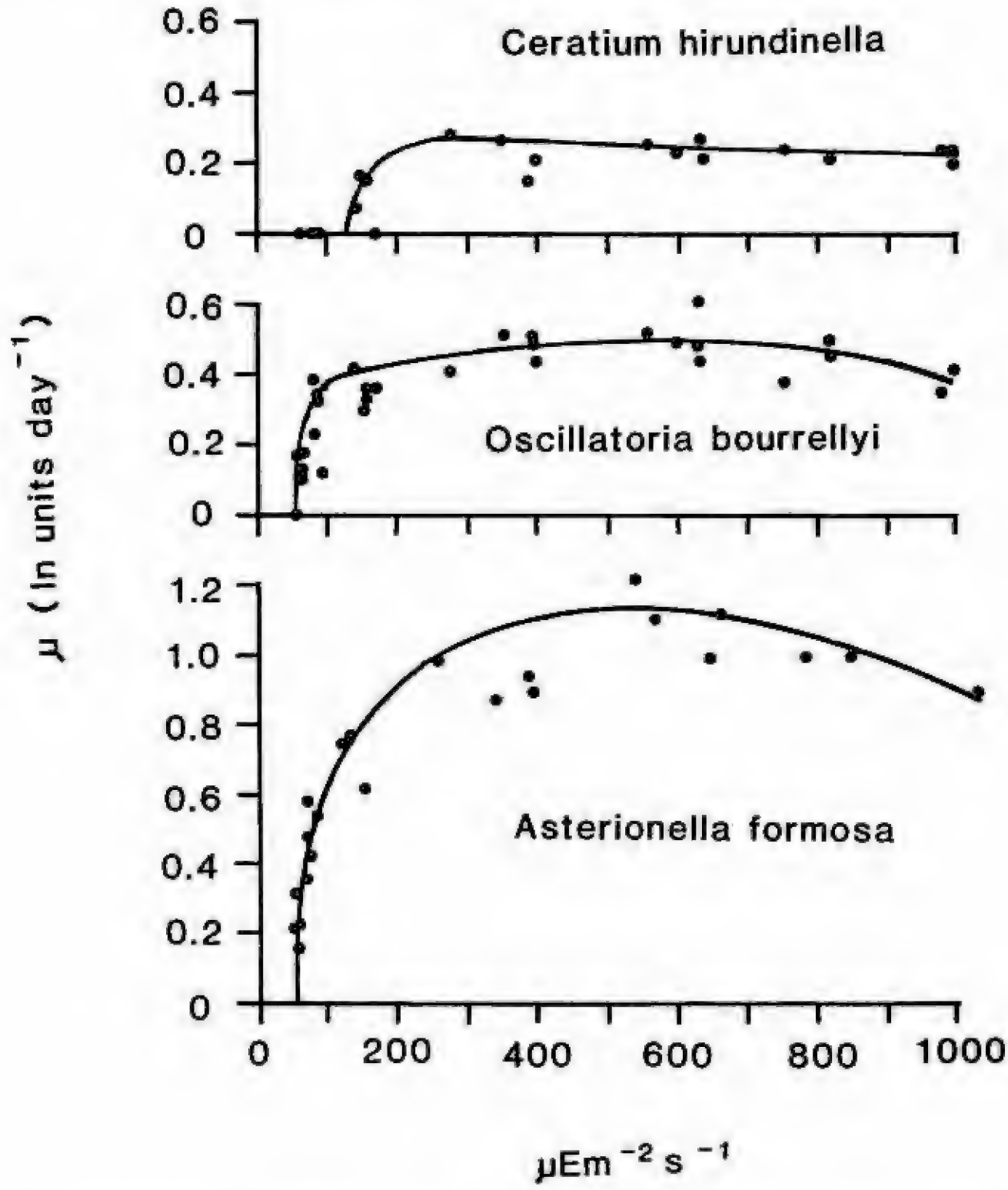

Figure 2

Growth rates of *Ceratium hirundinella*, *Oscillatoria bourrellyi*, and *Asterionella formosa* at different irradiances; cultures were grown at 20 ± 2°C under a 12:12 hour light:dark cycle.

Weather Induced Long-term Changes

A measure of the stability of the epilimnion or upper mixed layer during stratification is the value of N^2 (Mortimer 1974), i.e.,

$$N^2 = \frac{g}{\rho} \times \frac{\partial \rho}{\partial z} \tag{3}$$

where N is the Brunt-Väisälä frequency. Values were calculated weekly from temperature data for the 0–6 m layer from mid-June until the end of August from 1971–1983. The mean weekly values are given in Figure 3 together with the maximum summer biomass (as volume) over the 0–5-m layer for *Ceratium* and

diatoms (mainly ***Asterionella formosa*** Hass., ***Fragilaria crotonensis*** Kitton and ***Tabellaria flocculosa*** (Roth.) Kütz. var. ***asterionelloides***); the maximum biomass for ***Asterionellla*** during spring is given for comparison. Appreciable summer diatom populations were obtained only during cool windy years with weak stratification (mean weekly $N^2 < 5 \times 10^{-4}$ s $^{-2}$) as in 1974, 1980, 1981, whereas warm summers with well-developed stratification and high average N^2 as in 1975–79, 1982 and 1983 were characterized by the virtual absence of diatoms and large populations of *Ceratium*. The relatively poor production of *Ceratium* during 1983 was due to an unusual fungal epidemic during exponential growth (Canter and Heaney 1984). Interestingly this enabled the development of a dense population of ***Microcystis aeruginosa*** Kütz. emend. Elenkin.

Examination of all the individual summer diatom growths over this 13-year period showed no diatom increase with stability, as N^2, of greater than 4×10^{-4} s $^{-2}$.

Seasonal Changes

Algal growth during stratification depends not only on the degree of turbulent mixing but also on there being enough time for the interaction of other controlling factors. These include the depletion of major nutrients (Si, C, N, P) and the associated change of growth and sinking rates, losses due to grazing and parasitism, and the relative success of other species.

Both 1980 and 1981 provide good examples of cool windy summers with episodic, deep turbulent mixing and diatom growth. The annual population maxima of *Ceratium*, diatoms and blue-green algae in the 0–5-m layer are shown in Figure 4; also indicated are periods of high stability ($N^2 > 4 \times 10^{-4}$ s $^{-2}$), high pH/low CO_2 concentration (pH > 9.0), and silicon depletion, defined as insufficient dissolved silicon to support a population doubling (Si as $SiO_2 < 0.1$ mg $\cdot l^{-1}$). Summer diatom populations in both years show distinct maxima of varying frequency and amplitude which may be related to physical stability, nutrient depletion and parasitism. Periods of rapid diatom increase had little pronounced effect on the population cycle of *Ceratium* except in June 1981 after some exceptionally severe weather. Four of the diatom maxima (Fig 4 A–D) merit explanation:

A. In 1980, dry warm weather during April and May resulted in strong stratification and a decline of the diatom spring maximum to low numbers. By June and July, recovery of dissolved silicon and increased turbulence enabled diatom growth (***Asterionella*** and ***Tabellaria***) until limited by high pH/low CO_2 supply. The increased sinking rate observed in culture for ***Asterionella*** under CO_2 depletion ($\approx$1.0 m $\cdot$d $^{-1}$ (Jaworski et al. 1981)) would result in the rapid decline of diatoms in the lake during early August when stability increased.
B. During the middle of August 1980 there was a large, unexplained mortality of *Ceratium*, a deepening of the mixed layer, CO_2 resupply and renewed growth of ***Asterionella***, ***Tabellaria*** and smaller numbers of ***Fragilaria*** until limited by silicon depletion and fungal infection. All diatom species then declined and were replaced by a large growth of ***Anabaena*** spp.

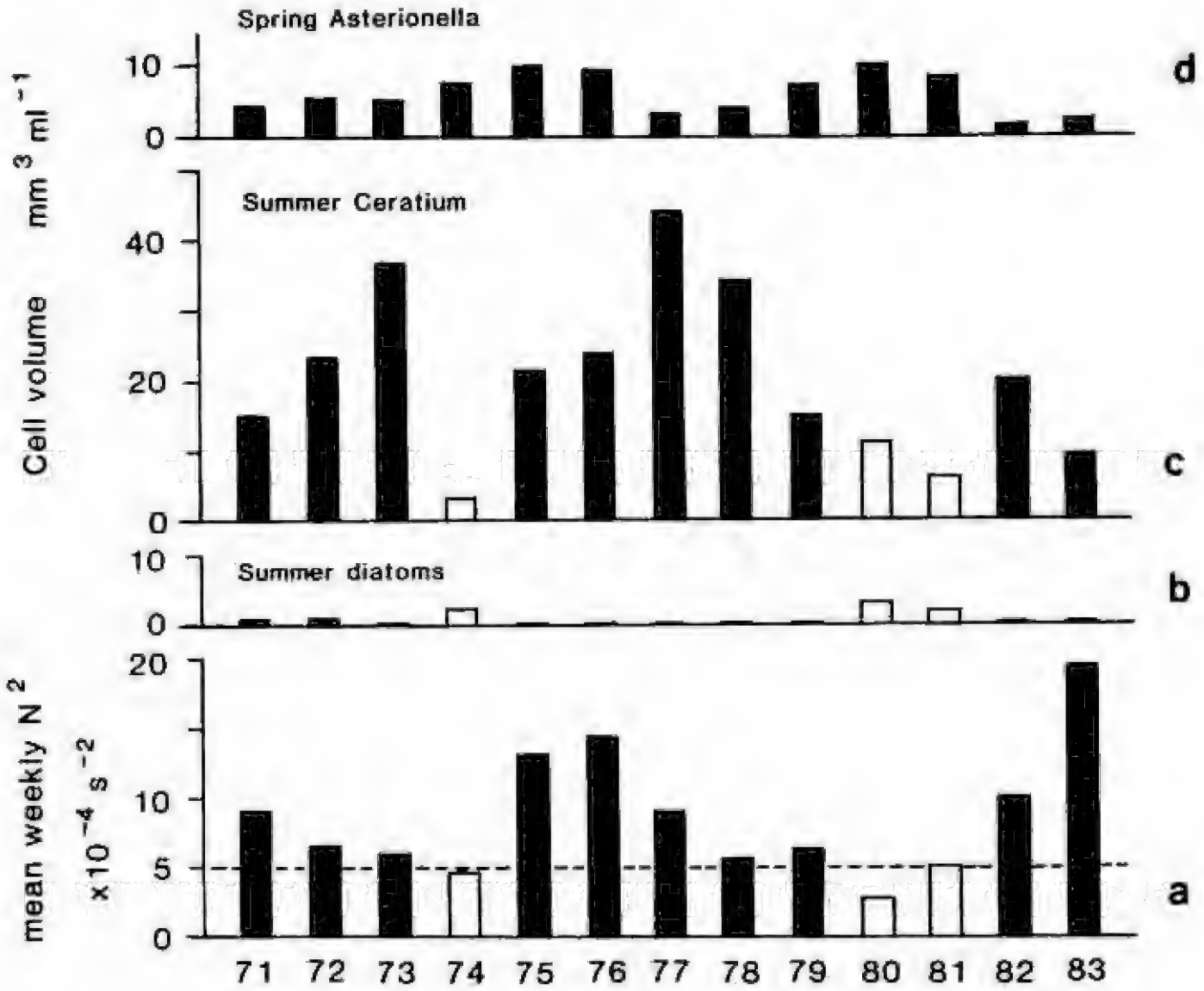

Figure 3

Relationship between (a) mean weekly stability (N^2) in Esthwaite Water (0–6-m layer) from mid-June until end of August, and maximum summer biomass (0–5-m layer) from beginning of July until end of August for (b) diatoms, and (c) ***Ceratium hirundinella***: (d) the maximum spring biomass for the usual dominant alga ***Asterionella formosa*** is given for comparison.

C. In contrast to 1980, April and May 1981 were cold and wet with almost complete mixing of the lake at the end of April. This resulted in a shallow decline of the spring diatoms. After a period of stability and silicon recovery there was another mixing episode in June with a large increase of ***Tabellaria*** until limited by silicon depletion. Rapid sedimentation followed with renewed water stability.

D. Further mixing in July and silicon renewal initiated a regrowth of ***Tabellaria*** until cessation in August due to conditions of high pH and low CO_2 concentrations. Physical stability, and high pH/low CO_2 concentrations due to photosynthesis of large populations of *Ceratium* and *Anabaena* spp. inhibited further summer diatom growth.

As well as major episodes of deep turbulent mixing described here, there is usually a regular daily wind pattern during anticyclonic weather in summer (George and Heaney 1978). These regular light-to-moderate morning and afternoon winds, with consequent mixing near the surface, prevent the formation of surface blooms of blue-green algae but may also favor *Ceratium* with its more effective depth regulation. Only at times of high mixing and rapid diatom growth during the summer (Fig 4) is

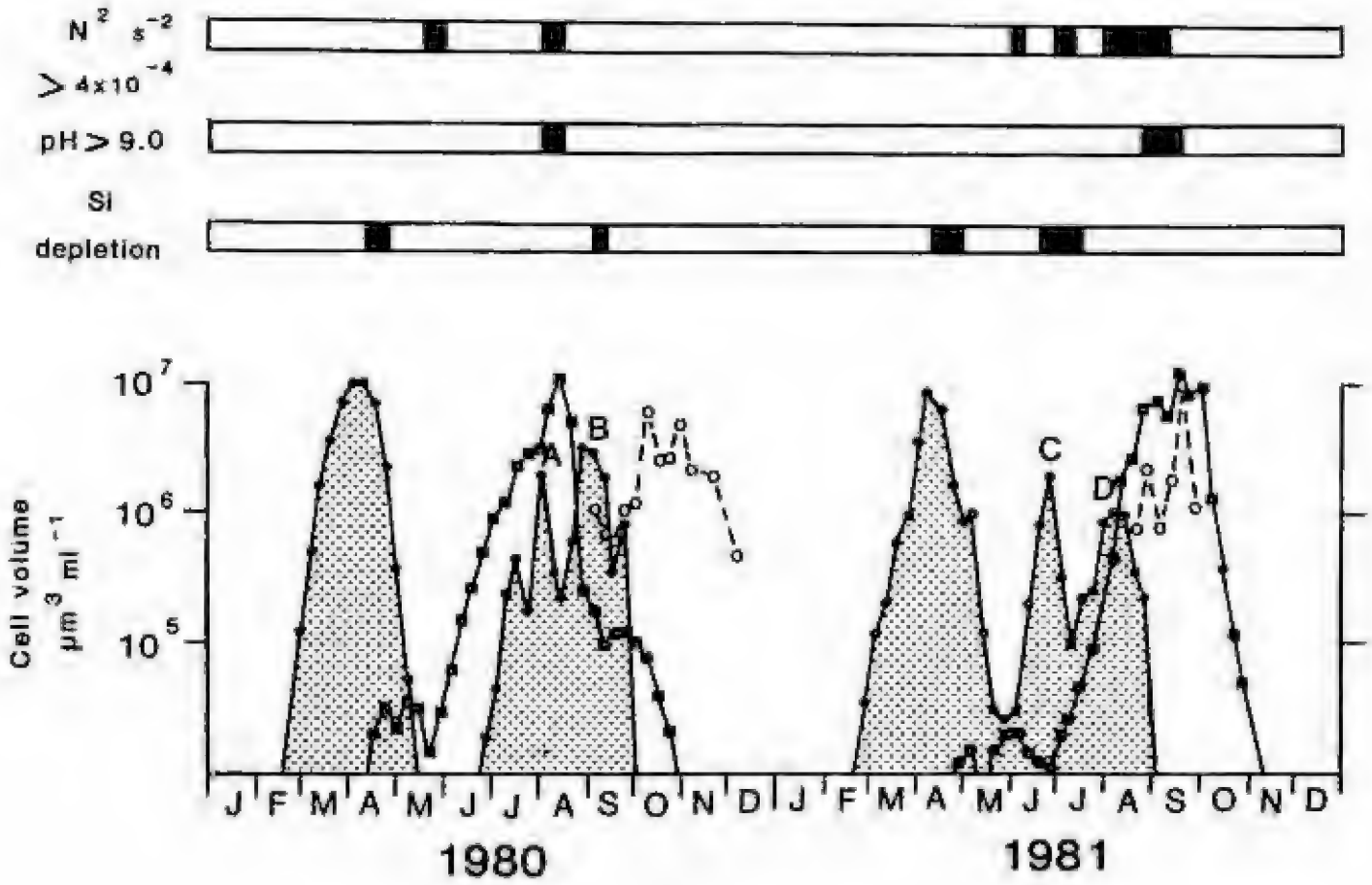

Figure 4

Annual population maxima as volume in the 0–5-m layer of Esthwaite Water in 1980 and 1981 for diatoms (stippled), dinoflagellates (box), and blue-green algae (o) in relation to periods of physical stability (N^2), (0–6-m layer), silicon depletion (insufficient silicon for a population doubling) and high surface water pH; the major summer diatom growths are indicated A–D.

there an indication of reduced growth rate of *Ceratium* populations. The cause of such depressions of *Ceratium* growth is not clear but may be due to impaired ability to depth-regulate to favorable light and nutrient conditions, or the direct interference with cell division by turbulence (Pollinger and Zemel 1981).

Rapid alterations of phytoplankton species composition due to physical mixing have been artificially induced in experimental enclosures in lakes by Reynolds, Wiseman, Godfrey and Butterwick (1983) with similar results to those obtained by natural mixing here. The critical value for N^2 of $0.4-5 \times 10^{-4}$ s $^{-2}$ which correlates with the resuspension and maintenance of diatoms in the upper mixed layer is similar to that found by Harris (1983) to occur during partial overturns in Hamilton Harbour, Ontario.

The present results illustrate the "tortoise and the hare" nature of phytoplankton assemblages in some shallow productive lakes where slow-growing algae that have rapid and precise depth regulation such as *Ceratium* can come to dominate over faster growing algae dependent upon turbulent mixing to maintain them in the euphotic zone.

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DIEL VERTICAL MIGRATION BY DINOFLAGELLATES: ROLES OF CARBOHYDRATE METABOLISM AND BEHAVIORAL FLEXIBILITY

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ABSTRACT

Some dinoflagellates are capable of sustained directed swimming, traversing about 10 m in the course of diel vertical migration. In coastal regions of the sea with stratified water columns, this behavior probably leads to enhanced growth. During the day, migrating dinoflagellates exploit high levels of irradiance near the surface, where low concentrations of inorganic nitrogen would normally limit growth; at night they descend to a layer where readily available nitrate is utilized to fulfill metabolic requirements. This process involves physiological as well as behavioral adaptations, because the uptake and assimilation of nitrate represents an unusually large metabolic demand during the dark period. An adaptation to diel irradiance, generally distributed among plants, is apparently capable of managing the special requirements of some migrating dinoflagellates: photosynthate is stored as carbohydrate during the day to be utilized at night to support the uptake and reduction of nitrate. A simple biochemical mechanism of source-sink regulation may have a central role in allocating photosynthate such that supply and demand are balanced over a diel cycle. Behavior of vertical migrators is flexible and tied to physiology so that behavior acts to regulate metabolism. The net result is optimization of growth rate within the constraints of an ecological strategy.

INTRODUCTION

In the context of migration, let us consider the dinoflagellates: the nature of their migration, the adaptive significance, and the physiological and behavioral mechanisms involved. Dinoflagellates are unicellular planktonic organisms capable of directed swimming by means of two flagella. A dinoflagellate, 50 μm in length, can sustain swimming velocities of 1 $m \cdot h^{-1}$ or more (e.g., Eppley, Holm-Hansen and Strickland 1968). In several dinoflagellate species, this swimming is directed into diel vertical migration (DVM), whereby a population will move vertically, phased to the diel cycle of solar irradiance (Forward 1976, Weiler and Karl 1979). This behavior commonly entails aggregation near the surface during the day and descent at night, with a vertical range on the order of 10 m. Vertically migrating populations of

dinoflagellates sometimes form red tides, the dense aggregations of algae that discolor coastal waters (Holmes, Williams and Eppley 1967). Although dinoflagelates undertake DVM in both the sea and freshwater under similar constraints, the work herein will mainly be concerned with events in coastal marine environments.

Several approaches have been employed to study the DVM of dinoflagellates. Observational studies (e.g., Hasle 1950, 1954 and references therein; Eppley et al. 1968; Blasco 1978) have provided the data from which hypotheses have been developed. As a result much has been learned of how the rates and timing of vertical migration are affected by environmental influences (cf. Eppley et al. 1968, Kamykowski and Zentara 1977, Heaney and Eppley 1981) and also how water movements such as internal waves or two-layer flows interact with vertical migration to promote the development of red tides or other ecologically important aggregations of dinoflagellates (Seliger, Carpenter, Loftus, Biggley and McElroy 1970; Kamykowski 1974; Seliger 1981; Brink, Jones, Van Leer, Mooers, Stuart, Stevenson, Dugdale and Hebum 1981).

Dinoflagellates are known to thrive where vertical gradients of light, temperature and nutrients are pronounced (Holmes et al. 1967, Margalef 1978). As a result, studies conducted in the laboratory have considered the biological responses of dinoflagellates to time-varying external conditions as determined by the migration of phytoplankters through vertical gradients. These studies have involved examining the physiology or behavior of dinoflagellates in response to light, temperature, salinity, or nutrients, varied individually (Hand, Collard and Davenport 1965; Harrison 1976; Forward 1976 and references therein; Kamykowski 1981a; Harding, Meeson and Tyler 1983). Results of such studies can be crucial in describing ecologically important phenomena. For instance, the avoidance of low salinity water by the red-tide dinoflagellate ***Prorocentrum mariae-lebouriae*** (Parke and Ballentine) Loeblich leads to confinement of a population in a subsurface layer that is transported from the southern Chesapeake Bay to the northern bay, where a bloom occurs annually (Tyler and Seliger 1978, 1981).

Recent work has demonstrated that in some ecologically relevant situations, the effects on DVM of any one environmental factor cannot be viewed in isolation: for example, several factors can strongly influence DVM simultaneously, as when nitrogenous nutrition substantially modifies the light- and temperature-dependent vertical movements of dinoflagellates grown in stratified water columns (Heaney and Eppley 1981; Cullen and Horrigan 1981). Progress in understanding the DVM of dinoflagellates thus depends on better appreciation of the action of all factors, internal and external, that influence the behavior and growth of migrating phytoplankton (Kamykowski 1979). Ideally, the functional relationships between interacting factors can be described so the behavior of dinoflagellates can be represented by simple but realistic models.

In this paper, I focus attention on the physiological correlates of DVM and postulate an underlying regulatory mechanism that may operate in a simple fashion to optimize the growth rate of vertically migrating phytoplankton within the constraints of the ecological strategies of different species. The interaction of light and nutrients

in affecting the behavior and growth of migrating phytoplankton can thereby be considered within a conceptual framework that encompasses both the holistic concept of "optimization" and a mechanistic description of biochemical regulation. It is hoped that this proposition will incite a fresh look at the interaction of light and nutrients in the context of migration of phytoplankton in natural waters.

THE ADAPTIVE ADVANTAGES OF DVM

It might be expected that DVM of dinoflagellates confers upon them some benefit in terms of net growth rate in the natural environment, this benefit being the "adaptive advantage" of DVM. The potential adaptive advantages of DVM can be divided into those that enhance the specific growth rate of the organisms and those that reduce losses due to predation, sinking or physical transport to regions unfavorable for growth. Indeed, it has been shown that the DVM of dinoflagellates, as it interacts with hydrographic motions, can produce a concentration mechanism that helps to maintain populations in specific environments (Seliger et al. 1970, Tyler and Seliger 1978, 1981; Kamykowski 1974, 1981b). Also, resistance to predation (Wyatt and Horwood 1973; Fiedler 1982; Huntley 1982) is clearly an adaptation that would enhance persistence of a population. Without detracting from the potential importance of these types of adaptations to the ecological success of dinoflagellates, I would like to focus on physiological mechanisms that might, in conjunction with DVM, enhance specific growth rates of phytoplankton. These mechanisms should be important because regardless of why dinoflagellates migrate, natural selection fosters physiological adaptations that maximize specific growth rates within the constraints of ecological strategies. Further, I choose to concentrate on the migration of dinoflagellates in stratified coastal waters nearshore, where red tides and other ecologically important aggregations of dinoflagellates can occur (e.g., Holmes et al. 1967, Tyler and Seliger 1981, Lasker 1975, Huntley 1982). An important characteristic of these coastal systems is a sharp gradient of nitrate concentration in the euphotic zone, within the range of vertical migration (e.g., Cullen, Stewart, Renger, Eppley and Winant 1983).

The Physiological Benefit of DVM

Although the potential influence of DVM on the growth of dinoflagellates has been studied, the subject has not been recently reviewed and a strong consensus on the physiological advantages of DVM has yet to be developed. Accordingly, a brief critique is in order.

Gran (1929) recognized that the motility of dinoflagellates enabled them to exploit the dissolved nutrients over a relatively large part of the water column, attaining in the process higher densities than nonmotile diatoms under conditions of stratification and nutrient depletion. Holmes et al. (1967) presented calculations which indicated that the concentrations of particulate nitrogen which were associated with red-tide blooms of dinoflagellates could develop only if dissolved nitrogen were taken

up through much of the water column and concentrated as cellular material by phototactic phytoplankton. A hypothesis was presented to explain how some dinoflagellates attain high concentrations in surface waters even though nitrate is depleted and the water is thus unable to support net growth of phytoplankton. At night, dinoflagellates descend to a layer where readily available nitrate is utilized to fulfill growth requirements; migration to the surface during the day produces visible blooms that are commonly observed (Holmes et al. 1967, Eppley et al. 1968). The optimization of growth rate is illustrated by considering the limitations which affect a nonmotile phytoplankter. In the surface layer, nutrients limit growth; if the organism grows where nutrients are adequate, light limits growth (Dugdale 1967). Nocturnal uptake of limiting nutrient is thus hypothesized as an important adaptive advantage of DVM (Eppley and Harrison 1975, Harrison 1976).

Tests of the hypothesis that nocturnal uptake of nitrate is important to migrating dinoflagellates have involved demonstration of the physiological capacity to assimilate nitrate in the dark and attempts to quantify the relative importance of light versus dark uptake of nitrate by populations of migrating dinoflagellates. Given the complexity of interacting factors that affect migratory phytoplankton in the sea, one would hope that experiments on populations in nature could resolve the validity of the hypothesis. Results of experiments in the field are the subject of some contention, however. Packard and Blasco (1974) and MacIsaac (1978) performed studies on a "natural population dominated by ***Gonyaulax polyedra***." Packard and Blasco's measurement of nitrate reductase activity suggested that ***Gonyaulax polyedra*** (Stein) has a special ability to assimilate nitrate in the dark: little diel variation in nitrate reductase activity was observed. In contrast, similar measurements on diatoms show a pronounced drop in nitrate reductase activity at night (Packard and Blasco 1974). It was also observed that the reduction of nitrite to ammonia could proceed with NADH as a cofactor rather than NADPH, as is common for algae and higher plants. Packard and Blasco pointed out that reduction of nitrate to ammonium was thus not tied to photosynthesis and could proceed at night. MacIsaac (1978) measured rates of nutrient uptake using the stable isotope ^{15}N as a tracer. She found that rates in the dark were clearly insufficient to support active growth of a population. In reference to the hypothesis that dinoflagellates have a special capacity for uptake of nutrients in the dark, she states that her results "do not support this hypothesis, nor does it appear that any special cellular characteristics beyond migration are required to explain occasions of dinoflagellate dominance." Recently, Dortch and Maske (1982) studied a bloom dominated by ***Gymnodinium sanguineum (splendens)*** K. Hirasaka, a motile, nonthecate dinoflagellate. They measured enzyme activities and rates of nitrate uptake and concluded that rates in the dark were significant and that the development of the population could probably be attributed to vertical migration and nocturnal uptake of nutrients.

The apparent conflict between MacIsaac's findings and those of others can probably be resolved by considering the types of measurement made and the environmental context. First, the coastal upwelling system off Baja California, site of the studies by Packard, Blasco, and MacIsaac (cf. Walsh, Kelley, Whitledge,

MacIsaac and Huntsman 1974), was much more energetic and less vertically stratified than the red-tide environments described by Holmes et al. (1967) and thus may represent a different but no less interesting situation in which dinoflagellates can outcompete diatoms (cf. Blasco 1977). It should be noted in this regard that despite the characterization of the population as dominated by ***Gonyaulax***, the organism constituted, on the average, much less than half the biomass of the phytoplankton, not the type of domination characteristic of red tides (Blasco 1977). Second, field measurements of nitrogen uptake utilized relatively large inoculations of tracer (10 μg-at $N \cdot l^{-1}$) so that in situ rates of uptake were not directly measured. Because a primary reason for the importance of nocturnal nutrition is the absence of external nutrients in surface waters during the day, in situ rates rather than maximal rates, are preferable data. The hypothesis concerning the relative importance of nocturnal nitrate uptake was therefore not tested in an entirely appropriate fashion.

Unlike experiments on natural populations, laboratory studies on cultures of dinoflagellates have produced clear-cut results. The red-tide dinoflagellate ***Gonyaulax polyedra***, grown in a light-dark cycle, could indeed satisfy its requirements for growth with nitrate taken up during the dark period (Harrison 1976). Experiments performed on cultures grown in 2-m water columns confirm that migrating populations of dinoflagellates can grow on inorganic nitrogen obtained during nocturnal descent. Evidence included disappearance of nitrate from the medium during the dark period (Cullen and Horrigan 1981) and a rapid increase of cellular N and subsequent continuation of growth after nocturnal exposure to nitrate (Heaney and Eppley 1981).

It should be noted that the perceived ability of an alga to take up and assimilate nitrate nocturnally can be in large part determined by the conditions under which the experiments are performed. For example, the migratory dinoflagellate ***Heterocapsa (Cachonina) niei*** (Loeblich III) Morill and Loeblich has been characterized as having a limited ability to take up and reduce nitrate at night (Hersey and Swift 1976). Consistent with this pattern, a synchronous culture of ***Heterocapsa*** exhibited no net synthesis of protein during the dark period of a diel cycle (Loeblich 1977). An experiment performed in our laboratory demonstrates that a modification of culture conditions can elicit a pronounced change in the magnitude of nocturnal nitrate assimilation. This is shown in Figure 1 where a culture of ***H. niei***, grown with adequate nitrate in the media, takes up about 60% less nitrate nocturnally as compared to during the day. After a short period of nitrate depletion, the culture readily takes up and reduces added nitrate either during the light or dark period. Vertical migration of ***H. niei*** into a nutrient depleted surface layer during the day may be analogous to our experimental manipulation in that it may induce sufficient internal nitrogen depletion to stimulate effective nitrate uptake at night (e.g., Harrison 1976). It is interesting that this response is not restricted to vertical migrators. Our results for a similar experiment on the diatom ***Skeletonema costatum*** (Greve.) Cleve were nearly identical (results not shown), and both sets of results were generally consistent with the observed responses of other types of microalgae such as ***Chlamydomonas*** and ***Dunaliella*** (Syrett 1981).

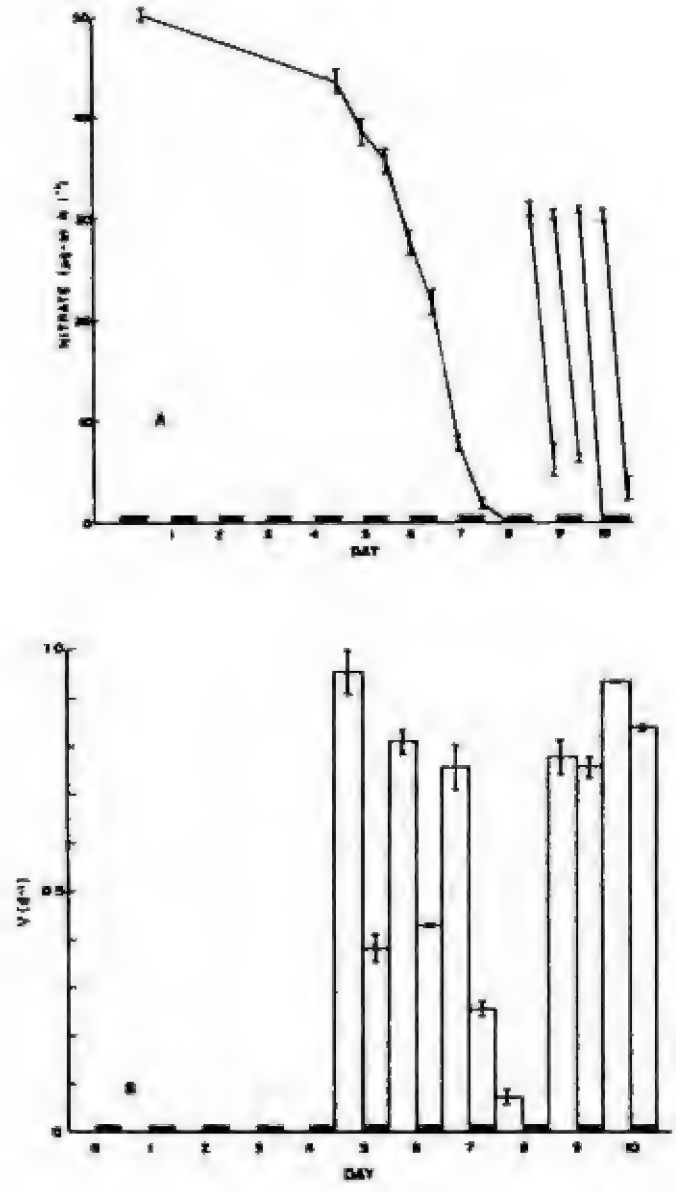

Figure 1

Diel pattern of nitrate uptake as affected by nitrogen depletion: *Heterocapsa niei*. Two cultures were grown at 20°C on a 12:12 light-dark cycle with photon flux density of 125 $\mu E \cdot m^{-2} \cdot s^{-1}$. All nutrients were present in excess except nitrate, which was initially 50 $\mu g-at\ N \cdot l^{-1}$.

A. Pattern of nitrate depletion: nitrate was depleted by day 8 and remained undetectable thereafter. On days 9 and 10, at the beginning of the light and dark periods, subsamples from the nitrate depleted cultures were inoculated with nitrate at 30 $\mu g-at\ N \cdot l^{-1}$. Concentrations at the beginning and end of each 12 h incubation period are plotted.

B. Rate of uptake: the specific rate of uptake of nitrate (v: μg-at nitrate-N taken up per μg-at cellular N per day) was calculated using an exponential model, $N_t = N_0 e^{vt}$ where N is cellular nitrogen (sum of the initial inoculum and the cumulative nitrate-N taken up), and t is 0.5 days. The dimension of v is d^{-1}. Measurements of intracellular nitrate + nitrite indicated that concentrations were sufficiently low to be ignored in these calculations. Error bars connect determinations for the two independent cultures, grown in parallel. Unpublished data of J.J. Cullen and Zhu Mingyuan.

Due to the severe limitations on experimentation on migrating populations at sea (Dortch and Maske 1982), an accurate description of the nutritional patterns of natural populations of migrating dinoflagellates will be difficult to obtain. Meanwhile, the hypothesis relating the success of some migrating dinoflagellates to the nocturnal uptake of nutrients should be retained.

PHYSIOLOGICAL CORRELATES OF DVM

As described above, diel vertical migration exposes the cell to an unusual type of environmental variability: a large diel variation of external nutrient concentration with a maximum at night. Such variation is exceptional if not unique with respect to phytoplankton. The diel pattern of nutrition, with nitrate uptake predominantly in the dark, is equally unusual. From an evolutionary perspective, one might suggest the DVM has been selected for in these dinoflagellates because they can take up nitrate in the dark. Considering experimental results demonstrating the inducibility of nocturnal nitrate uptake (Fig 1 and Syrett 1981), one could propose the alternate hypothesis that the nocturnal uptake of nitrate by dinoflagellates can be attributed primarily to their ability to migrate vertically. These hypotheses can be addressed by identifying the physiological correlates of DVM and considering the degree to which observed patterns represent specialized physiological adaptations to DVM rather than normal responses to an unusual regime of environmental variability imposed by DVM. An examination of the responses of plants to a diel-varying environment is illuminating in this context.

Unicellular algae and higher plants have adapted to spending about half their lives in the dark by maintaining metabolic processes in the absence of light at the expense of photosynthetic products stored during the day. A manifestation of this adaptation is a diel cycle in the concentration of starch or some other carbohydrate (Preiss and Levi 1979; Cook 1966; Eppley, Holmes and Paasche 1967; Loeblich 1977; Foy and Smith 1980; Fig 2). The regulation of starch synthesis is thus a subject of special interest because it is clear that regulatory processes are effective in matching the diurnal accumulation of starch to the nocturnal demand. Geiger and Giaquinta (1982) and Challa (1976) have shown that in the leaves of some higher plants the rate of accumulation of carbohydrate is inversely related to the length of the photosynthetic period such that relatively greater quantities of carbohydrate are available for longer nights. Experiments conducted on blue-green algae yield similar results (Foy and Smith 1980). These observations support a hypothesis that the accumulation of carbohydrate results from a "programmed synthesis that is influenced by the energy demand of the diurnal dark period" (Chatteron and Silvius 1979). This hypothesis is relevant to the study of dinoflagllate migration because assimilation of nitrate represents a large demand for metabolites (reductant, carbon skeletons and ATP; Syrett 1981, p. 201): according to the hypothesis, the diurnal accumulation of carbohydrate should be dependent to some extent on the amount of nitrate assimilated at night; in turn, nocturnal nitrate assimilation depends on storage products such as carbohydrate.

It is instructive to think in terms of a source-sink balance, well recognized in the plant literature but incompletely understood (Wareing and Patrick 1975). The source is photosynthesis and the sink, broadly speaking, is metabolism and growth. When considering the leaves of higher plants, a major sink is sucrose for export through the phloem (Geiger and Giaquinta 1982), whereas in unicellular algae, the synthesis of protein is typically the important end product (Myers 1951).

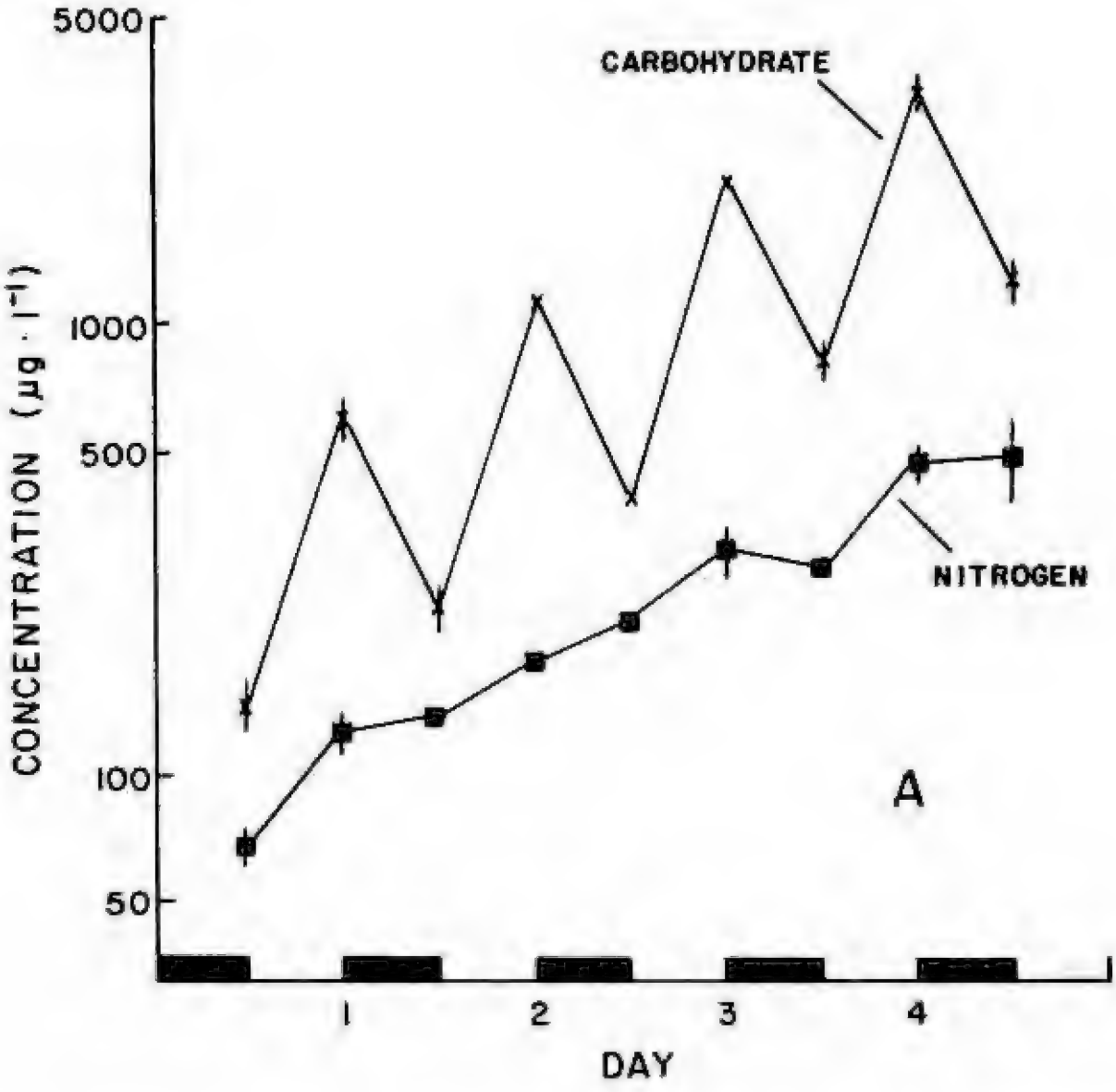

Figure 2

Diel variation in carbohydrate content of plants grown on light : dark cycles. ***Heterocapsa (Cachonina) niei***, a dinoflagellate which is known to migrate but is considered to have a limited ability to assimilate nitrate at night (Hersey and Swift 1976, Loeblich 1977): ×, carbohydrate (dextrose equivalents, phenol-sulphuric acid method); filled boxes, particulate nitrogen (micro-Kjeldahl method). Logarithmic transform: error bars represent the 95% confidence limits for carbohydrate, and the range of duplicates for nitrogen (when the range exceeds the dimension of the symbol). Culture conditions as in Fig 1, except nitrate was present in excess. Unpublished data of Zhu Mingyuan and J.J. Cullen.

Empirical evidence consistent with source-sink regulation in the allocation of photosynthate is plentiful. The C/N ratio in algae is responsive to the ratio of source (photosynthesis) to sink (nitrogen assimilation and concurrent protein synthesis) in a pattern that of course reflects the relative rates of carbon assimilation and nitrogen assimilation but which also facilitates restoration of a typical C/N balance upon return to optimal conditions after a period of deprivation (cf. Myers 1951; Eppley and Renger 1974; Lehman and Wober 1976; Morris 1981; Syrett 1981; Rivkin, Voytek and Seliger 1982). The plasticity of C/N is attributable in large part to accumulation and mobilization of carbohydrate, although Fogg (1959) implicates lipid. Carbohydrate is accumulated in response to nutrient depletion or to increments of supersaturating light intensity (source exceeds sink), and it is degraded in darkness, in the absence of CO_2, or when adequate nutrients are restored after nitrogen depletion (sink exceeds source). Similarly, in the leaves of higher plants, starch levels also respond to

experimentally imposed changes in the source-sink balance. After other leaves in the plant are shaded to increase demand for sucrose, starch levels in the lighted leaf decline in a reversible response (Thorne and Koller 1974), whereas when a leaf is removed to minimize sinks for photosynthesis, starch is accumulated in the leaf at a greater rate than when attached (Heldt, Chon, Maronde, Herold, Stankovic, Walker, Kraminer, Kirk and Heber 1977).

Biochemical studies of the regulation of starch formation are consistent with the notion that the accumulation of carbohydrate is governed by a source-sink balance. Central to the regulatory scheme is the ratio of 3-phosphoglycerate (PGA) and other photosynthetic intermediates to inorganic phosphate (P_i) in the chloroplast (Preiss and Levi 1979, Heldt et al. 1977). If the utilization of photosynthetic intermediates for metabolic processes is less than the production by photosynthesis, PGA accumulates and the production and storage of starch is stimulated; if the demand for intermediates exceeds the supply, starch will be degraded and utilized. As far as the primary products of photosynthesis are concerned, drains to sucrose or protein synthesis may act equivalently, given that an efficient shuttle (Heldt and Rapley 1970; Kelley, Latzko and Gibbs 1976; Heldt et al. 1977) promotes transfer of PGA, triosephosphates and P_i across the chloroplast envelope, thus assuring unobstructed communication between source and either sink (cf. Bassham and Buchanan 1982). It is thus reasonable to assume as a working hypothesis that source-sink regulation of carbohydrate metabolism, essentially as described for higher plants (and cyanobacteria: cf. Lehman and Wober 1976, Foy and Smith 1980), applies to microalgae in general.

Specifically, I would like to suggest that this nonspecialized biochemical mechanism is sufficiently flexible to support the physiological correlates of DVM, enhanced storage of carbohydrate during the day and significant uptake and assimilation of nitrate at night at the expense of carbohydrate. This mechanism of source-sink regulation bridges the temporal gap between dark and light metabolism such that photosynthesis during the day can affect nitrate assimilation at night and nocturnal nutrition can determine the allocation of photosynthate during the day. According to the source-sink hypothesis, when migration through a subsurface nutricline forces a diel cycle on the availability of nitrate, nitrogen deficiency during the day should stimulate the accumulation of carbohydrate (Mykelstad 1974; Haug, Myklestad and Sakshaug 1979), concurrently enhancing the capacity for sustained uptake and reduction of nitrate in the dark. If inorganic nitrogen is depleted throughout the water column, accumulated carbohydrate is not mobilized at night and the carbohydrate content and C/N of the population will rise dramatically in a well-recognized response to depletion of nitrogen (Strickland, Holm-Hansen, Eppley and Linn 1969; Heaney and Eppley 1981; Cullen and Horrigan 1981). As discussed later, there are behavioral as well as physiological responses to sustained nutrient limitation.

Few data are available to examine directly the regulation of metabolism during DVM. However, some preliminary observations (J.J. Cullen and Zhu Mingyuan, unpublished) are consistent with the principles of source-sink regulation as outlined above. A culture of ***Heterocapsa niei***, grown at 20°C, L:D 12:12, with nitrate as a nitrogen source (Fig 3A), displays a regular diel pattern of carbohydrate : nitrogen

content indicative of balanced growth over 24 h, which was accomplished by matching the diurnal accumulation of carbohydrate to the nocturnal demands. Immediately after nitrogen is depleted from the media, relative synthesis of carbohydrate during the day is enhanced (as might be expected, given that N is unavailable) and nocturnal utilization of carbohydrate is reduced, due presumably to the restriction of catabolic activity by N-depletion. The net result is a rapid, substantial increase in carbohydrate : nitrogen comparable to that observed in numerous studies on the effects of nitrogen depletion (e.g., Haug et al. 1979). Exposure of subsamples from the nitrogen-depleted culture to nitrate at 30 $\mu g\text{-at} \cdot l^{-1}$ resulted in vigorous uptake and reduction (Fig 1) and concomitant changes in carbohydrate metabolism (Fig 3B and C). Net synthesis of carbohydrate was reduced if nitrate was added at the beginning of the light period and consumption of carbohydrate in the dark was greatly enhanced by the addition of nitrate at the beginning of the dark period.

By comparing the magnitude of nocturnal nitrate uptake with the amount of excess carbohydrate utilization associated with the uptake (Fig 3B and C), a rough stoichiometry can be calculated (Table 1): for each nitrate ion taken up and reduced, about 6 CH_2O units of starch are utilized, theoretically enough to supply the necessary electrons, ATP, and carbon skeletons for assimilation of nitrate to cell proteins (cf. Syrett 1955, Raven and Beardall 1981). Some aspects of source-sink regulation are thus illustrated. The presence of a nitrogen source during the day affects the degree to which carbohydrate accumulates, and the nocturnal utilization of carbohydrate is to a large extent dependent on the uptake of nitrate. These data are not sufficient to demonstrate that enhanced diurnal accumulation of carbohydrate associated with nitrogen depletion is necessary to fuel nocturnal nitrate assimilation associated with vertical migration through a nitrate gradient. Experiments to test this hypothesis are underway.

It is noteworthy that the behavioral patterns of some vertical migrators seem to be closely linked to physiological responses to nutrition. Laboratory experiments have shown that when nutrients are replete throughout the water column, vertical migration is such that the maximum time is spent near the surface, within the constraints of completing nocturnal descent. When nitrate is depleted in the surface layer, behavior is modified to provide more exposure to nutrients at depth while still maintaining a high rate of photosynthesis during the day. ***Gonyaulax polyedra*** increases its exposure to nutrients by beginning its nocturnal descent early (Heaney and Eppley 1981), whereas ***Gymnodinium sanguineum (splendens)*** restricts its diurnal ascent to a subsurface layer, often close to the nitracline, in which light intensity is approximately saturating for photosynthesis (Cullen and Horrigan 1981). When nitrogenous nutrients are not available within the range of vertical migration, the pattern of migration in ***Gonyaulax polyedra*** is modified further such that it no longer migrates to the surface during the day. These behavioral changes occur when excess carbohydrate accumulation as depicted in Figure 3A would be expected. It is possible then, that changes in behavioral patterns are directly associated with changes in chemical composition or physiological state. Better studied are the responses of cyanobacteria

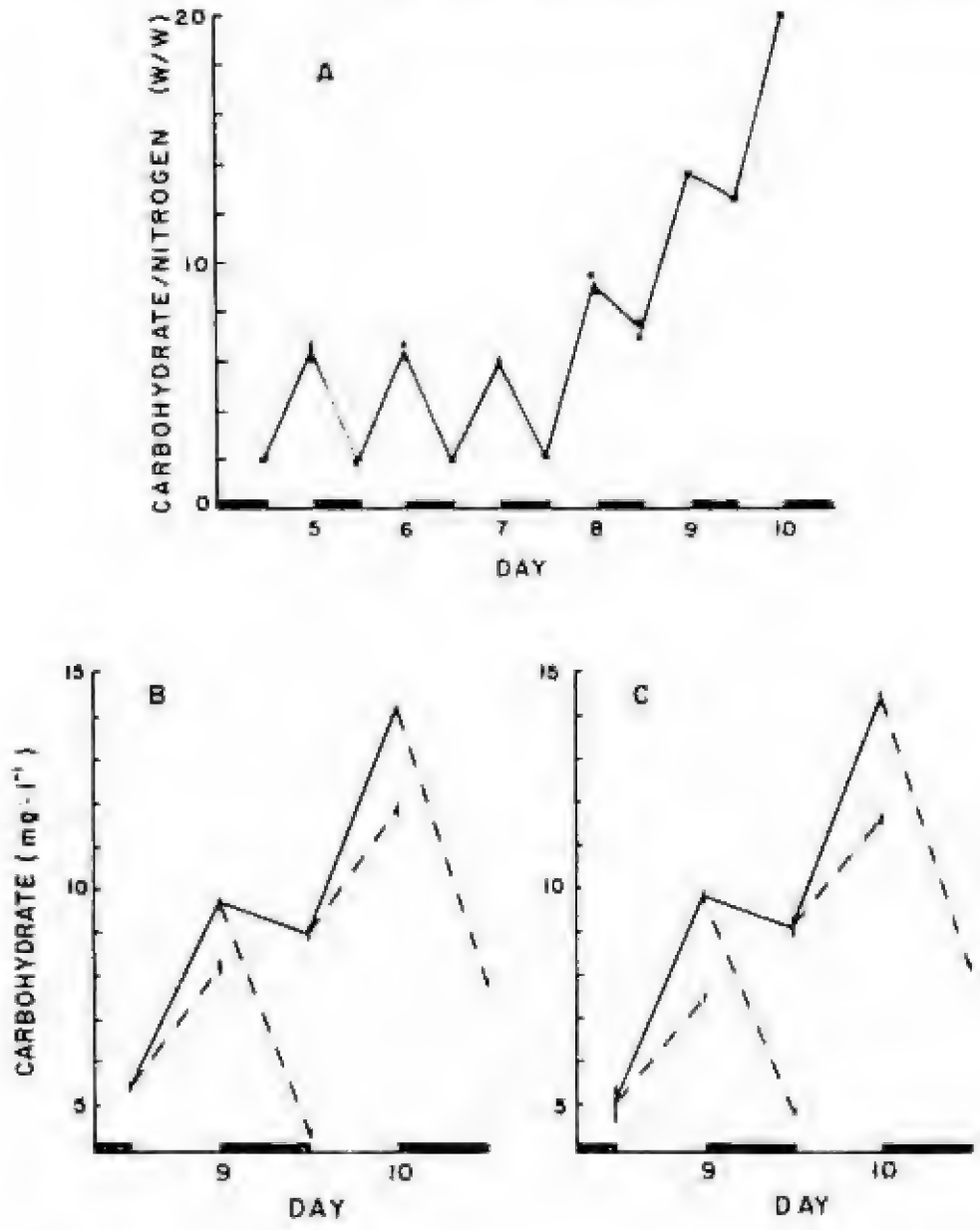

Figure 3

Diel variation of carbohydrate content of ***Heterocapsa niei*** as affected by nitrogenous nutrition. Same experiment as described in Fig 1.

A. Carbohydrate/nitrogen (ratio by weight): o and x are independent replicate cultures. Carbohydrate measured by the phenol-sulphuric acid method. Nitrogen, as nitrate, was depleted from the media on day 8. Cellular nitrogen was determined from the disappearance of nitrate, by difference.

B,C. Carbohydrate concentration after nitrogen depletion on independent replicate cultures. Solid line represents nitrogen-depleted culture as in A; dashed line represents subsample exposed to 30 $\mu g-at \cdot l^{-1}$ nitrate. Vertical bars indicate standard error of the mean. Unpublished data of J.J. Cullen and Zhu Mingyuan.

(see Klemer 1985 for a detailed discussion). When excessive accumulation of carbohydrate is stimulated, downward movement results (Oliver, Utkilen and Walsby 1983; Klemer 1985), which decreases irradiance and increases the likelihood of encountering nutrients. When conditions encourage the depletion of stored carbon (adequate nutrients, subsaturating irradiance), upward movement is observed. The response of some cyanobacteria to CO_2 depletion might represent an unfortunate consequence of source-sink regulation. Accumulation at the surface in nuisance blooms occurs, perhaps because the biochemical manifestation of CO_2 limitation is similar to that of insufficient light, in that the supply of photosynthetic intermediates does not meet the metabolic demand.

Table 1

Utilization of carbohydrate during the dark period in the presence and absence of nitrate. The experiment was performed on nitrogen-depleted cultures of ***Heterocapsa niei***, day 9 (see Figs 1,3). Pairs of numbers are determinations for independent replicate cultures.

		1200 h	2400 h	Decrease
CONTROL	Carbohydrate ($\mu g \cdot l^{-1}$)	9760, 9908	9024, 9166	736, 732
	Nitrate (μg-at $N \cdot l^{-1}$)	0, 0	0, 0	0, 0
EXPERIMENTAL	Carbohydrate ($\mu g \cdot l^{-1}$)	9760, 9908	4417, 4868	5343, 5040
	Nitrate (μg-at $N \cdot l^{-1}$)	30.61, 30.07	6.13, 6.50	24.48, 23.57

DEFINITION OF "EXCESS" CARBOHYDRATE UTILIZATION: (decrease in experimental) − (decrease in control) = 4607, 4298 $\mu g \cdot l^{-1}$

MOLAR RATIO OF EXCESS CARBOHYDRATE UTILIZED TO NITRATE TAKEN UP: 6.27, 6.08

The intraspecific patterns in migratory behavior can thus be linked to relative fluxes of light and nutrients. How can interspecific patterns be explained? One possibility is that the thresholds for behavioral response to source-sink imbalance differ between species according to ecological strategy. (1) On one extreme might be ***Gonyaulax polyedra***, which can tolerate very high irradiance and low nitrate during the day so long as a source of adequate nutrients is encountered at night to support growth and to utilize stores of carbohydrate (e.g., Heaney and Eppley 1981). It appears that photosynthate can be stored to a considerable extent before behavior is substantially affected. (2) ***Gymnodinium*** may represent an intermediate case. When nutrients are not available in the surface layer, the organism avoids high light intensities (which would stimulate excessive storage of carbohydrate, cf. Cook 1966) and aggregates at a lower light level that is still nearly saturating for photosynthesis (Cullen and Horrigan 1981). Nonetheless, nitrate is taken up to a significant extent at night, so a good deal of source-sink imbalance is accommodated. (3) Phytoplankters that aggregate in well-defined strata but do not undergo significant diel migration (e.g., in some instances, ***Ceratium tripos*** (O.F. Muller) Nitzsch; Eppley, Reid, Cullen, Winant and Stewart 1984) would, according to the source-sink hypothesis of behavioral regulation, tolerate relatively little imbalance in the fluxes of photosynthate and nutrients before adjusting vertical position. Diurnal variation of chemical composition would thus be minimal and accordingly, assimilation of nutrients would be in large part light-driven, i.e., nocturnal assimilation of nitrate would be relatively unimportant. Each of these strategies represents an ecological trade-off that would be effective in a restricted range of environmental conditions.

Although one is limited to speculation in discussions of mechanisms by which behavior interacts with physiology to regulate the growth rate of vertically migrating dinoflagellates, it is possible to define clearly the adaptive significance of behavioral flexibility in the natural environment. By linking behavioral plasticity to physiological state, some environmental stresses are avoided. In stratified coastal waters (cf. Eppley and Harrison 1975, Cullen and Eppley 1981) a source of adequate nutrients will be found within the relatively shallow euphotic zone; by shifting migrational patterns downward in response to nutrient depletion, migrating dinoflagellates in coastal waters need not deal with high irradiance *and* nutrient starvation (cf. Prézelin 1982). Likewise, because adequate nitrate is available within the range of migration of populations in the lower euphotic zone, vertically migrating phytoplankton need not adapt to low irradiance without a source of nutrients available (cf. Prézelin and Matlick 1983).

SUMMARY AND CONCLUSIONS

It has been demonstrated that plants have developed simple regulatory mechanisms that tend to optimize the allocation of photosynthate for maximal growth; as a result, enough carbohydrate is synthesized and stored during the day to satisfy nocturnal metabolic needs. In stratified waters characteristic of many coastal environments, vertically migrating phytoplankton stand to benefit greatly from such a strategy. During the day, they can migrate into well-lighted but nutrient-poor strata where the storage of carbohydrate would be stimulated by both high irradiance and low nutrient concentration. At night, they can descend to water rich in nutrients where the processes of nutrient uptake and assimilation depend on storage products. Because dinoflagellates differ in their abilities to take up and assimilate nutrients in the dark (Hersey and Swift 1976) and also differ in their patterns of vertical migration (Eppley et al. 1984 and references therein), it is likely that physiological and behavioral patterns are coordinated, making behavior an important aspect of metabolic regulation. Indeed, available data indicate that nutrient-dependent modification of vertical migration acts to enhance growth of some dinoflagelates; that is, the nutritional status of the phytoplankters profoundly influences their vertical migration such that their overall pattern of vertical displacement supports balanced supply rates of photosynthate and nutrients. Behavioral repertoires differ between species, apparently reflecting ecological trade-offs, but in each case demonstrating that in dinoflagellates migrational patterns are altered to avoid the stresses of limiting nutrients or overly high irradiance.

Note added in proof: Interspecific variation in dark nitrogen uptake by dinoflagellates is discussed in a recent paper by Paasche, Bryceson, and Tangen (Journal of Phycology 20: 394-401, 1984).

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NUTRIENT-INDUCED MIGRATIONS OF BLUE-GREEN ALGAE (CYANOBACTERIA)

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ABSTRACT

Buoyancy changes in blue-green algae result in vertical migrations during periods of water column stability. The buoyancy status of these prokaryotic microorganisms depends on relative rates of photosynthesis and nutrient-limited growth. Light affects not only photosynthesis but also nutrient uptake. Nitrogen and phosphorus can limit relative gas vacuolation (buoyancy) as well as growth, and carbon can limit the extent of negative buoyancy responses as well as the incorporation of nitrogen and phosphorus into compounds necessary for gas vacuole synthesis. In a stratified lake, blue-green algae tend to show negative buoyancy responses to surface conditions (high light—nutrient poor) and positive responses to deep water conditions (low light—nutrient rich). As lake enrichment proceeds, migrations between deep, nutrient-rich layers and the surface become more frequent, surface blooms persist, and finally blue-green algae may envelop the photic zone.

INTRODUCTION

In most aquatic environments, the growth of photosynthetic microorganisms is determined primarily by the availability of light and nutrients. In thermally stratified bodies of water, light is, of course, more available in the upper or near-surface layers, whereas nutrients tend to be more available in the lower, less well-illuminated layers. Consequently, in stratified water columns, phytoplankton populations are often nutrient limited near the surface and light limited toward the base of the photic zone. As nutrients are exhausted in the surface layers, many phytoplankters experience increases in specific gravity and in sinking rate, but once in dimmer, nutrient-rich layers, they exhibit decreases in specific gravity that slow their sinking rate or, in the case of blue-green algae, may render them positively buoyant. The buoyancy status of diatoms (Steele and Yentsch 1960) as well as blue-green algae (Klemer 1973, 1976; Walsby and Klemer 1974) has been shown to vary directly with the availability of certain nutrients and inversely with light intensity. Such buoyancy responses by blue-green algae are of interest because they are largely responsible for the success of this

group in waters undergoing eutrophication. When positive, these responses may promote the formation of the intense surface blooms characteristic of blue-green algae in eutrophic lakes.

As enriched lakes proceed from oligotrophy through mesotrophy to eutrophy, depth profiles of photosynthesis and phytoplankton abundance can change in a manner similar to that diagramed in Figure 1. Often such a pattern of change is due to invasion and then dominance of the open water of a lake by blue-green algae. During the course of eutrophication, the phytoplankton community changes from one that is primarily nutrient limited to one in which light becomes the overriding limiting factor. In most oligotrophic lakes, blue-green algae are not an important part of the phytoplankton, although some may be present at the sediment-water interface. In such lakes, the phytoplankton is sparse and develops no large population maxima at any depth in the water column. As lakes become richer in nutrients, blue-greens such as ***Oscillatoria rubescens*** may occur in layers at the base of the photic zone near the nutrient-rich hypolimnion or bottom water (Hasler 1947). In the later stages of eutrophication, blue-greens are frequently dominant throughout the photic zone by midsummer, but in the transition from mesotrophy to eutrophy, these algae may appear only occasionally at the surface. Blue-green algal accumulations at the surface, at the base of the photic zone and at intermediate depths in a stable water column as well as migrations between those depths require buoyancy regulation.

MECHANISMS OF BUOYANCY REGULATION

Factors Affecting Buoyancy

Perhaps the most sensitive buoyancy regulation yet studied in blue-greens is that exhibited by metalimnetic populations of ***Oscillatoria***. These algae can migrate within a narrow range of depths near the base of the photic zone (Konopka 1982). Short-range migrations by algae in such stratified situations provide them with access to adequate nutrients below as well as sufficient light above metalimnetic layers. Walsby and Klemer (1974) obtained the first evidence of positive and negative buoyancy responses below and above, respectively, a stratified population of ***Oscillatoria***. They took *O. **agardhii*** var. ***isothrix*** from a metalimnetic layer in Deming Lake, Minnesota, and resuspended the alga in 1-liter bottles at 1-meter intervals with and without additional nitrogen (0.07 mM N). After two days, determinations of buoyancy indicated decreases with the alga suspended at higher light intensities above the layer and, with N-enriched alga, a buoyancy increase when suspended below the layer. Thus displaced from its position in counter gradients of light intensity and nutrient concentrations, the alga exhibited buoyancy changes that would have taken it toward its original position. This experiment also provided evidence of a light-nutrient interaction in buoyancy regulation by a blue-green alga. Buoyancy did decrease at the higher light intensities toward the surface. But at every depth, the alga was more buoyant in bottles enriched with N, and only with N enrichment did an actual increase in buoyancy occur.

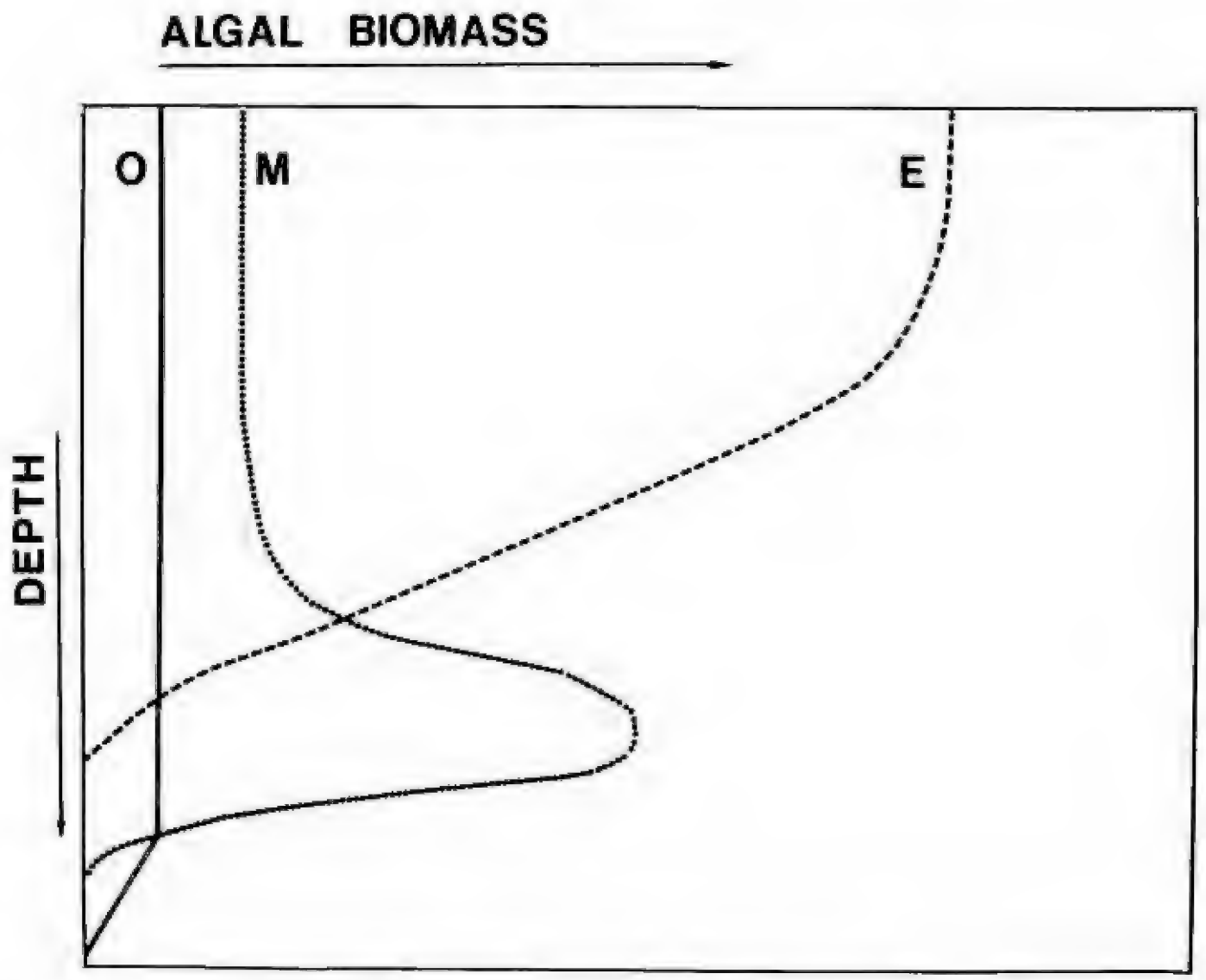

Figure 1

A classic progression in the vertical distribution of algal biomass featuring oligotrophic (O), mesotrophic (M) and eutrophic (E) stages in the history of an enriched lake. For example, Lake Zurich from the summer of 1895 to that of 1936 (Hasler 1947). Metalimnetic population maxima are not peculiar to mesotrophic lakes; they may, in fact, develop weakly in oligotrophic lakes.

As part of the same study, Walsby and Klemer examined the buoyancy status of several subsamples of the *Oscillatoria* population, each with a different percentage of its gas vesicles collapsed, and they found a close relationship between buoyancy status and the degree of gas vacuolation. With all of their gas vesicles intact, a majority of the filaments of *Oscillatoria* were positively buoyant, but with about 25% of the gas vesicles collapsed, the filaments were, on average, negatively buoyant. Thus the degree of gas vacuolation could have been the primary determinant of buoyancy status in the *O. agardhii* var. *isothrix* population in Deming Lake. Gas vacuoles are aggregates of vesicles with gas-permeable, proteinaceous walls. The vesicles have cylindrical walls and conical ends; they are about 65 nm to 75 nm in diameter and from about 100 nm to over 1000 nm in length (Smith and Peat 1967, Walsby 1977). These vesicles collapse under pressure, and in some planktonic blue-green algae, increases in cell turgor pressure can collapse their weaker vesicles (Dinsdale and Walsby 1972, Walsby and Klemer 1974, Konopka 1982).

The Role of Light Intensity

Buoyancy regulation in blue-green algae has been related to changes in turgor pressure, in relative rates of growth and gas-vesicle synthesis and in the amount of "ballast" molecule accumulation. The first environmental factor to be implicated in such changes was light intensity. Walsby (1969, 1970) observed that ***Anabaena flos-aquae*** became more buoyant at low light intensities, and he associated low rates of photosynthesis and growth with gas-vesicle accumulation and buoyancy increases. Light intensities, appropriate for such buoyancy increases, occur at the base of the photic zone in the metalimnion or upper hypolimnion of a stratified water column or in the mixed portion of a water column if mixing is sufficiently deep or water sufficiently turbid, that is, if mean light intensity is low enough. Once positively buoyant in a stable water column, an alga can move up into higher light intensities that may promote higher rates of photosynthesis and a loss of buoyancy.

Light-Nutrient Interactions

Walsby considered two possible mechanisms by which relative gas vacuolation (RGV) might decrease with increased light intensity. The alga's gas vesicles might be diluted by rapid growth (growth-rate mechanism) or weaker gas vesicles might be collapsed by turgor pressure increases resulting from "excess" photosynthesis, photosynthesis in excess of nutrient-limited growth (Walsby 1970, 1971; Dinsdale and Walsby 1972). Subsequently Grant and Walsby (1977) demonstrated that an accumulation of osmotically active photosynthate contributes to the rise in turgor pressure associated with gas-vesicle collapse in *Anabaena*, and Allison and Walsby (1981) discovered that potassium accumulation does likewise. Walsby's turgor-collapse mechanism allows for light-nutrient interactions because the availability of limiting nutrients can determine the rate of photosynthate assimilation, and, hence, the light intensity at which photosynthesis becomes excessive and photosynthate begins to accumulate.

Ballast Molecule Accumulation

In accord with the turgor-collapse mechanism, a positively buoyant alga would rise in a stable water column until enough gas vesicles had collapsed as a result of increases in light intensity, photosynthesis, and turgor pressure to render the alga neutrally or negatively buoyant. However, blue-greens capable of collapsing enough gas vesicles to become negatively buoyant do not always do so once at the surface, and some blue-greens have gas vesicles that are too strong to collapse by turgor pressure (Walsby 1978; Walsby, Utkilen and Johnsen 1983). The former may remain buoyant because of specific nutrient effects to be discussed later; the latter may regulate buoyancy with cellular ballast in the form of polysaccharides or other dense molecules (Oliver, Utkilen and Walsby, Abstracts, IV International Symposium on Photosynthetic Prokaryotes, Bombannes, France 1982). With regard to the latter, it

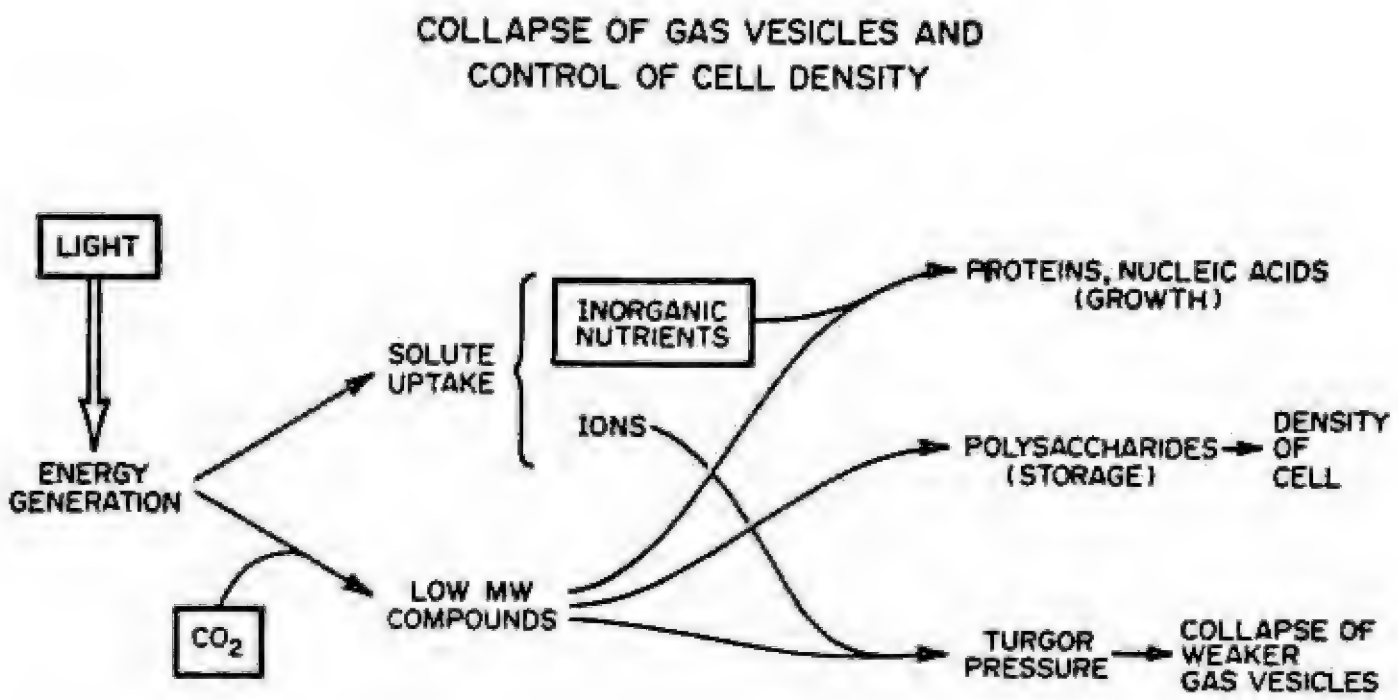

Figure 2

Relationships between factors important to buoyancy regulation by planktonic blue-green algae (from Konopka 1984).

has been known for some time that nutrient limitation (e.g., N limitation) can promote carbohydrate accumulation in algae (Syrett 1962). Moreover, Konopka (1981) found that polysaccharide accumulation in ***Oscillatoria*** from a metalimnetic population increased directly with temperature, but only after exposure to a light intensity ten times greater than the in situ light intensity. More recently Gibson (1984) reported that the carbohydrate : protein ratio of phytoplankton increased towards the surface of stratified water columns. Gibson related this increase primarily to light intensity but also to temperature. Thus the same factors, light intensity and nutrient limitation, that can reduce buoyancy in some algae by increasing turgor pressure and reducing RGV may also reduce buoyancy by promoting the accumulation of carbohydrate ballast. In blue-greens with turgor-resistant gas vesicles, ballast regulation may be the principal means of buoyancy regulation. Konopka (1984) has very clearly summarized what is known of light-nutrient interactions that can account for the turgor-collapse of gas vesicles as well as the accumulation of ballast molecules. As shown in Figure 2, the balance between photosynthesis and nutrient-limited growth potential determines whether the carbon fixed in photosynthesis flows largely into amino acids, nucleotides and other "building blocks" for growth and gas vesicle synthesis, or whether it accumulates as low molecular weight compounds that raise turgor pressure and thereby

collapse gas vesicles, or as polysaccharides that act as cellular ballast. In nutrient-limited cells, much of the light energy captured by blue-greens is used to accumulate ions (K^+), osmotically-active photosynthate or polysaccharide—all of which can act to reduce buoyancy. In nutrient-sufficient cells, on the other hand, more of this energy is used in nutrient assimilation and more recently fixed as well as stored carbon is incorporated into building blocks for growth and gas vesicle synthesis; thus, turgor pressure is not increased, carbon stored as polysaccharides is mobilized, and buoyancy is maintained or perhaps increased.

Nutrient-Specific Effects on Buoyancy

As mentioned above, algae, even those with gas vesicles weak enough to be susceptible to a turgor-collapse mechanism, do not always show a reduction in buoyancy as they approach higher light intensities near the surface. Although light is frequently referred to as the primary or overriding environmental factor in algal buoyancy regulation, light effects on buoyancy in blue-green algae can depend on nutritional status. For example, CO_2-deprived ***Anabaena flos-aquae*** showed no reduction in RGV upon exposure to increased light intensity (Dinsdale and Walsby 1972), and N-limited ***Oscillatoria rubescens*** showed no increase in RGV upon transfer to reduced light intensity (Klemer, Feuillade and Feuillade, unpublished) or to darkness (Klemer 1978).

The role of limiting nutrients in buoyancy regulation by blue-greens is not as clear-cut as that of light appears to be. Inorganic carbon (C_i), nitrogen (N) and phosphorus (P) have all been suspected of limiting growth or photosynthesis in such a way that RGV either failed to decrease or actually increased as algae gathered at the surface (Reynolds and Walsby 1975). In fact, the effect of C_i limitation on buoyancy in blue-greens is quite different from that of N and P. Unlike C_i, both N and P invariably limit RGV in the process of limiting the growth of ***Oscillatoria***. The RGV of ***O. rubescens*** grown in N-limiting chemostats decreased with transitions to lower dilution rates and more severe N limitation (Klemer 1978), and in N-limiting and P-limiting cyclostats at steady state, the RGV of ***Oscillatoria*** varied directly, not inversely, with the availability of N and P (Klemer 1983; Feuillade, Feuillade and Klemer, unpublished). On the other hand, RGV did increase with transitions from N-limiting to CO_2-limiting conditions in cyclostat cultures of ***O. rubescens*** (Klemer, Feuillade and Feuillade 1982). Whereas Dinsdale and Walsby (1972) had demonstrated that CO_2 deprivation could impair the turgor collapse mechanism and prevent a light-induced reduction in the RGV of ***Anabaena flos-aquae***, the work with ***O. rubescens*** showed that RGV could actually increase during CO_2 deprivation and could do so despite increases in mean light intensity as the optical density of the CO_2-limited cyclostat cultures decreased. Hence in forming a bloom, ***Oscillatoria*** might show an increase in buoyancy in response to CO_2 or light limitation, but not in response to N or P limitation. These generalizations regarding specific nutrient effects on buoyancy are consistent with the buoyancy regulation scheme outlined in Figure 2. N and P limitation of growth can promote an increase in osmotically-active photosynthate

(turgor pressure) and/or in polysaccharide ballast, whereas C_i limitation can have an opposite effect with respect to both the turgor-collapse and the cellular-ballast mechanisms. However, these mechanisms may not apply to all blue-green algae as they apply to ***Anabaena*** or ***Oscillatoria***. ***Microcystis aeruginosa*** seems to be one exception (Booker and Walsby 1981).

Negative Versus Positive Regulation of RGV and Buoyancy

The turgor-collapse mechanism is best understood as a negative means of controlling buoyancy and in the ways in which CO_2 or light limitation can impair its operation during bloom formation. We do know that each of the conditions or sets of conditions associated with increases in the relative gas vacuolation of planktonic blue-green algae (light limitation, C_i limitation, N-enrichment of N-limited cells) also favors relative protein synthesis (Klemer, Feuillade and Feuillade 1982). However, we do not know how or to what extent the synthesis of gas-vesicles is controlled, nor do we fully understand how light intensity and nutritional status interact to affect buoyancy in algae adapted to different combinations of those factors. Hence it is perhaps premature to attempt to explain the strategic significance of buoyancy regulation. I am not suggesting that we refrain from constructing working hypotheses as a basis for experimental work, but that we refrain from making sweeping generalizations that may explain the purpose of mechanisms so eloquently that they impede our understanding of how those mechanisms work. Even some of the more obvious advantages of buoyancy regulation may, if focused on too narrowly, lead to such a generalization. The strategies discussed in the next section should be considered no more than working hypotheses.

ADAPTIVE SIGNIFICANCE OF BUOYANCY

Regulation in Blue-green Algae

Buoyancy regulation by blue-greens clearly provides them with better access to light and nutrients in a stratified water column than other nonflagellated phytoplankton have. Fogg and Walsby (1971) discussed this advantage with respect to the formation of metalimnetic layers poised at optimal depths in counter gradients of light intensity and nutrient concentrations and in regard to migrations between well-lighted and nutrient-rich layers. But the adaptive significance of buoyancy regulation may well depend on the "trophic" circumstances. In the early stages of eutrophication, blue-greens are more likely to dominate the metalimnion of a stratified lake; only in the later stages does blue-green algal dominance of the epilimnion become persistent. A classic case history of lake eutrophication is that of the Untersee basin of the Zurichsee (Lake Zurich). Between 1895 and 1936 *Oscillatoria rubescens* populations developed from a sparse presence to significant metalimnetic layers and then to surface blooms during the summer (Hasler 1947). This transition from metalimnetic to epilimnetic dominance is very instructive in its adaptive significance.

The Role of Carbon in Bloom Formation

Phytoplankton ecologists and physiologists have noted several possible advantages to buoyancy regulation that permits occupation of the surface layer of a stratified water column. Walsby (1970) indicated the possible significance of the fact that bloom-forming algae have the advantage of better access to atmospheric CO_2. Recently, Paerl and Ustach (1982) have emphasized this particular advantage. They showed that ***Aphanizomenon flos-aquae*** and ***Anabaena circinalis*** photosynthesize faster and may be less buoyant with CO_2 than with other forms of inorganic carbon, and suggested that surface scum formation is a means of assuring access to CO_2, the preferred form. Klemer and Grover (unpublished) compared the effects of HCO_3^- and atmospheric CO_2 on the RGV of ***Oscillatoria rubescens*** taken from a C_i-limiting chemostat, and observed reductions in buoyancy that differed only in the speed of the response. Alga with access to atmospheric CO_2 showed decreases in RGV within 6 hours, whereas alga supplied with HCO_3^- (4 mM) in capped vials achieved slightly greater reductions in the interval between 7 and 29 hours. In other laboratory and in lake experiments, C_i additions as HCO_3^- and CO_3^{-2} have resulted in reductions in the buoyancy and in the surface population density of blue-green algae. In experiments with ***Anabaena flos-aquae***, Booker and Walsby (1981) found that $NaCO_3$ enrichment reduced the buoyancy of the alga in stoppered bottles as well as the amount of surface accumulation in a laboratory water column. In lake experiments, blue-green algal responses to HCO_3^- enrichment have varied. For example, the addition of HCO_3^- was followed by a more rapid reduction in the intensity of a natural ***Anabaena*** bloom within treated columns than within similarly isolated control columns of lake water (Klemer and Brasino, unpublished). However, the addition of HCO_3^- to a N- and P-induced bloom of *O. **agardhii*** var. ***isothrix*** permitted the bloom to intensify for several days before it collapsed (Klemer, Pierson and Whiteside 1985).

Recent Deming Lake Experiments

In an on-going series of experiments on Deming Lake, Minnesota, a lake with a relatively low surface alkalinity (0.5 $mEq \cdot l^{-1}$), we have studied the effects of various forms of enrichment with C_i, N and P on metalimnetic populations of ***Oscillatoria agardhii*** var. ***isothrix***. The first of these experiments involved blooms that were induced by N and P enrichment of only the metalimnetic portion of isolated water columns. The ***Oscillatoria*** in those water columns began to move up from the metalimnion before the transparency of the surface water was significantly reduced. Thus the buoyancy response was primarily a nutrient effect, not a response to reduced light intensity. We then considered the possibility that N and P enrichment had produced the blooms by inducing C_i limitation of photosynthesis and thereby impairing negative buoyancy regulation. To test this hypothesis, we added $NaHCO_3$ to the surface water of one of two isolated water columns in which simultaneous blooms were underway (exp. 1); to the upper 4 m of four water columns, two with and two without additional N and P (N to the upper 4 m, P to the metalimnion—exp. 2); and

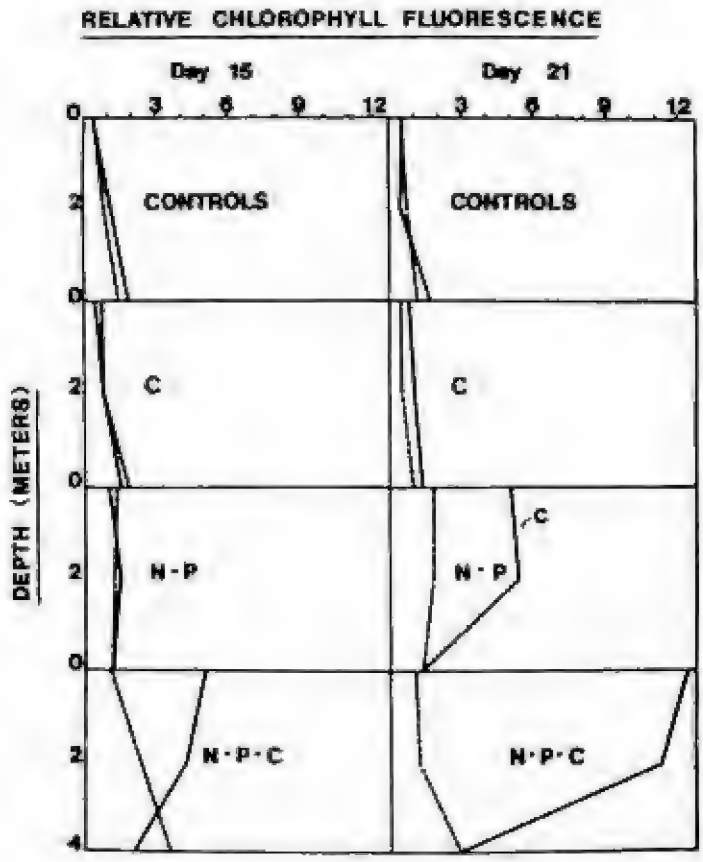

Figure 3

Depth profiles of relative chlorophyll fluorescence in eight isolated water columns 15 and 21 days after initial addition of 2 mM $NaHCO_3$, 0.71 mM NH_4Cl and 0.03 mM KH_2PO_4 in the indicated combinations. By day 15, one of the two tubes treated with N+P+C (broken line) had exchanged surface water with the lake, and on day 16, one of the two tubes enriched initially with N and P only (solid line) received 2 mM $NaHCO_3$. Sampling was restricted to the upper 4 m to avoid disruption of the algal layer concentrated around 5 m.

to the upper 4 m of four water columns, two with and two without N and P added to the metalimnetic layers (exp. 3). In the first experiment, the addition of HCO_3^- to one of two simultaneous blooms was followed by an intensification of both blooms and then a more rapid collapse of the treated bloom (Klemer, Pierson and Whiteside 1985). In the second experiment of this series, HCO_3^- enrichment increased N uptake and intensified blooms in N- and P-enriched water columns instead of deterring their formation or causing their collapse (see Figure 3). During the third experiment, we restricted N and P enrichment to the metalimnion as in the first experiment, but we provided the N and P in graded concentrations with and without 2 mM $NaHCO_3$ added to the upper 4 m. As a result, *Oscillatoria* moved to the surface much faster in the HCO_3^- enriched columns and bloomed more intensely and persistently with higher concentrations of N and P. Each of these experiments included unenriched control water columns and none of these produced surface blooms (Klemer, Detenbeck and Grover, unpublished). This study is still in progress but the data in hand do warrant some tentative conclusions. The amount of N and P available may not only determine the likelihood of C_i limitation of photosynthesis in a low alkalinity lake, but it may also determine the nature and magnitude of buoyancy responses by C_i-limited blue-green algae to increased C_i availability. If N and P sufficiency is marginal, C_i enrichment may lead to N or P limitation and a reduction in buoyancy. However, if N and P are present in great excess, increases in C_i may increase N and P utilization and

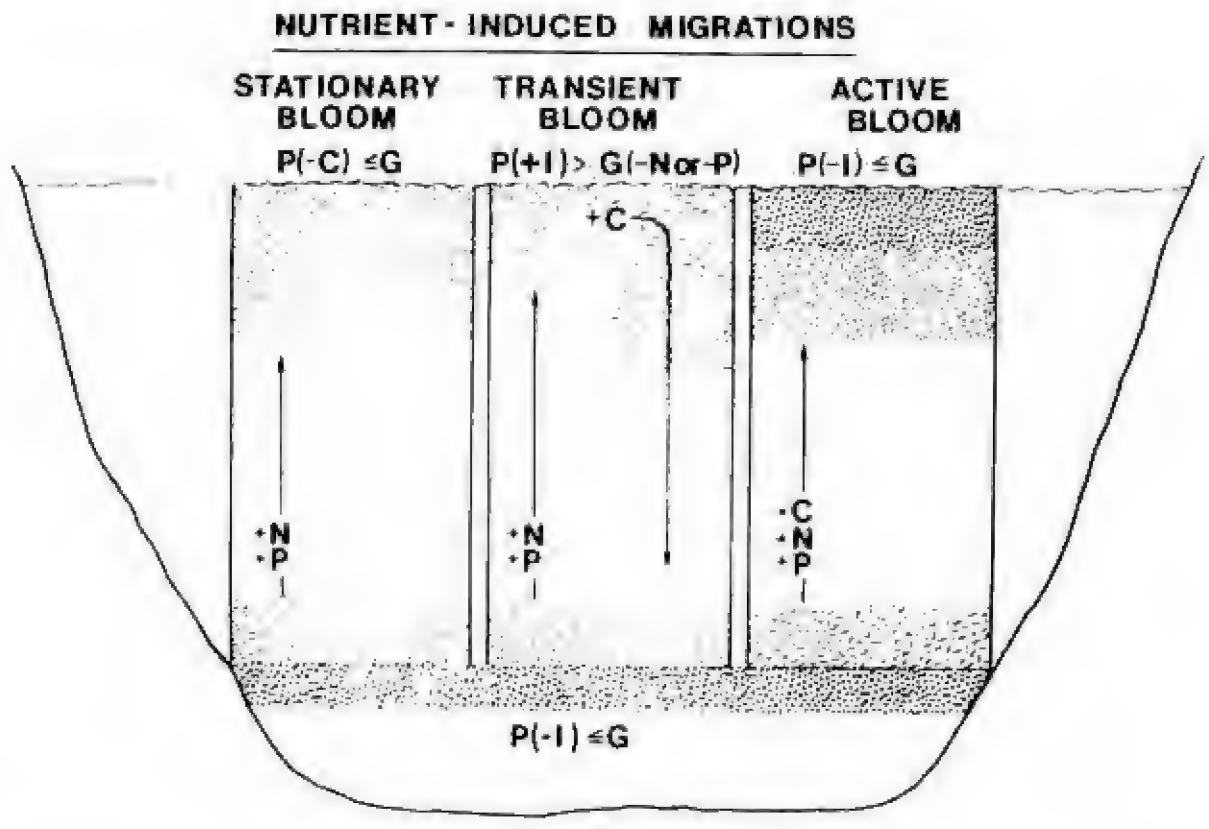

Figure 4

Three types of surface blooms by metalimnetic populations of *Oscillatoria agardhii* var. *isothrix* induced within isolated water columns by the addition of C_i, N and P in different combinations and sequences. Toward the base of the water columns, photosynthesis (P) is light limited (−I) and less than or equal to the nutrient-limited growth potential (G); this condition produces neutrally or positively buoyant algae. In the stationary bloom, photosynthesis (P) is C_i limited (−C) and again less than or equal to the nutrient-limited growth potential (G). In the transient bloom, photosynthesis (P) is greater than the nutrient-limited growth potential (G). Here, photosynthesis proceeds until nutrient limitation develops and buoyancy reduction occurs. In the active bloom, migration and growth proceed until photosynthesis (P) becomes light limited (−I).

may intensify blooms, perhaps to the point that self-shading becomes a major factor in maintaining buoyancy.

Working Hypotheses

As stated above, the buoyancy status of blue-greens depends on the balance between photosynthesis and nutrient-limited growth. When, under light or C_i limitation, the rate of photosynthesis limits growth, the alga will be buoyant. As light or C_i levels increase, the buoyancy response of the alga will depend on whether or not it remains nutrient (e.g., N or P) sufficient. As shown in Figure 4, the series of experiments in Deming Lake produced three types of blooms. Blooms induced by N and P enrichment of the metalimnion persisted, at times, for a week or more without increasing very much in intensity. These more or less stationary blooms were probably C_i limited. Other N- and P-induced blooms, including that in a column supplied with C_i only at the surface, and those in columns with C_i added to the upper 4 m and with lower concentrations of N and P added to the metalimnetic layers were transient in nature and probably became N or P limited. The third type of bloom was active in the sense that it continued to intensify until the Secchi disc transparency decreased to less

than 0.5 m and light limitation became a major factor contributing to its persistence. This type of bloom occurred with C_i enrichment of the upper 4 m of a water column and the addition of higher levels of N and P (0.71 mM N and 0.03 mM P) to the metalimnion or to both the upper 4 m (N) and the metalimnion (P).

The responses depicted in Figure 4 can be related to changes in the vertical distribution of blue-greens during the course of lake eutrophication. In the early stages of eutrophication, nutrient concentrations adequate for the growth of blue-greens may occur only in the deeper layers of a thermally stratified lake, that is, near the chemocline. Blue-greens do well in this niche not only because they can regulate their buoyancy, but also because they have very efficient pigment systems that can harvest those parts of the spectrum of photosynthetically active light that are available at the base of the photic zone. As the nutrient concentrations at the chemocline increase or as the chemocline rises, blue-greens become more and more able to move toward the surface; but what's in it for them? The buoyancy of highly gas-vacuolate blue-greens can give them greater access to atmospheric CO_2 (Paerl and Ustach 1982) and perhaps even to atmospheric fixed N (Lewis 1983), but a demand for C_i or N (-C_i or N limitation, that is) is not essential to an increase in RGV or buoyancy. In fact, N limitation can have a negative effect on buoyancy, and C_i enrichment can promote bloom formation by N- and P-rich algae. If forced to attribute a strategy to the behavior of bloom-forming blue-greens, I would maintain that, in the later stages of eutrophication, their buoyancy regulation allows them to extend their dominance into the surface layers where they can monopolize incident radiation and reduce the photic zone to a layer containing their surface populations. N-fixing blue-greens, of course, can usually make this move once the phosphorus supply is sufficient. Blue-greens are able to envelop the photic zone because, with sufficient nutrients, they can balance photosynthesis and growth so as to maintain buoyancy as they approach the surface. Limitation of photosynthesis by light or C_i can affect this balance; both may be involved to some extent at some stage, but neither is essential to bloom formation.

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DIFFERENTIAL MIGRATION OF CRYPTOPHYCEAE IN LAKE CONSTANCE

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ABSTRACT

Several species of the genera *Rhodomonas* and *Cryptomonas* are at times dominant contributors to total phytoplankton biomass in Lake Constance. Their growth periods largely coincide. Diurnal studies have shown vertical migrations that lead to increasing concentration of the different populations close to their light optima during the course of the photoperiod. Nevertheless, under field conditions a considerable degree of overlap remains between the different species, which is probably due to redispersal by turbulence. Exposition experiments with 2 m long plexiglass tubes, in which turbulence is strongly reduced, yielded a more pronounced segregation. Four out of five species were found to migrate. As shown by growth experiments, depth distribution seems to be mainly light controlled. Separation along the vertical gradient is discussed as a possible mechanism of reducing interspecific competition between species associated along the time gradient.

INTRODUCTION

One of the major selective advantages of flagellates over immotile algae is their capacity for vertical migration in a sufficiently stable water column and thus their ability to exploit vertical gradients. In stratified lakes there is always a gradient of light and sometimes a gradient of temperature and nutrients with depth. This study attempts to analyze the differential migration patterns of five closely related cryptophyte species in relation to light.

The study was performed in Lake Constance, a warm-monomictic, subalpine lake in Central Europe of 500 km^2 surface area and 250 m maximum depth. The lake is rich in nutrients (P_{tot} at spring overturn about 100 $\mu g \cdot l^{-1}$) and stratified from April on. The seasonality of the dominant physico-chemical environmental variables is given by Stabel and Tilzer (1981). The analysis of Cryptophyte migration presented here was restricted to a period when the temperature gradient was less than 3°C (a range smaller than temporal variability within the study period and too slight to be of physiological importance) along the migratory range (surface to 10 m depth) and

nutrients were available at nonlimiting concentrations throughout the entire water column.

Cryptophyceae are represented in Lake Constance by five different species: ***Rhodomonas minuta*** Skuja, ***Rhodomonas lens*** Pascher et Ruttner, ***Cryptomonas marssonii*** Skuja, ***Cryptomonas ovata*** Ehr., ***Cryptomonas rostratiformis*** Skuja (Fig 1). ***R. minuta***, ***R. lens***, ***C. marssonii***, ***C. ovata*** are important contributors to algal biomass during the vernal bloom usually observed in May. After a clear-water phase in June, induced by excessive grazing, ***C. ovata*** and ***C. marssonii*** have a second growth pulse in early summer. At the same time the annual maximum of ***C. rostratiformis*** is observed (Sommer 1981). Smaller growth pulses of these species occur whenever intrusion of hypolimnetic water has lead to a phosphorus enrichment of the euphotic zone. Only ***R. lens*** is completely restricted to winter and spring. Under calm weather conditions, four of these five species tend to be stratified, with ***C. marssonii***, ***C. rostratiformis*** and ***R. minuta*** restricted to the upper half of the euphotic zone and ***R. lens*** to the lower half. The vertical distribution pattern of ***C. ovata*** is variable and often unclear. In 1980 the first of a series of diurnal studies provided the opportunity to study the differential migration of the two ***Rhodomonas*** species. Unfortunately, subsequent 24-h cruises were performed under conditions of strong water movements which, by the combination of lateral advection and phytoplankton patchiness, led to erratic results. Therefore, I decided to study the differential migration in in situ tubes, in which redispersal by turbulence could be considered minimal and resampling of the same population was guaranteed. The migration experiments were combined with in situ growth experiments to compare phototactic behavior with physiological light requirements.

METHODS

Vertical migration was studied in plexiglass tubes of 2-m length and 8-cm diameter. At 20-cm intervals there were outlets for sampling. Thus the depth distribution of the algae could be resolved at 20-cm intervals. Exposure started on the evening before the experimental day in order to allow the tubes to adjust to the outside temperature before the start of phototactic migration. The tubes were filled with mixed water samples which were integrated from 0- to 4-m depth and were gently mixed to guarantee random distribution of the flagellates at the start. An umbrella was used to protect phytoplankton from exposure to full sunlight. One tube (I) was exposed at 0- to 2-m depth and the other (II) at 2- to 4-m depth. From the 1980 study I knew that vertical segregation increases with increasing exposure time to light. The lowest index of overlap between ***R. minuta*** and ***R. lens*** had been recorded for 1900 h (Sommer 1982). On the other hand, it was also desirable that even species with high light requirement should find their preferred light intensity throughout the course of the experiment. Therefore, only bright days were chosen and half-time between noon and sunset was taken as the end point of experiments. Samples were preserved immediately by addition of Lugol's iodine solution.

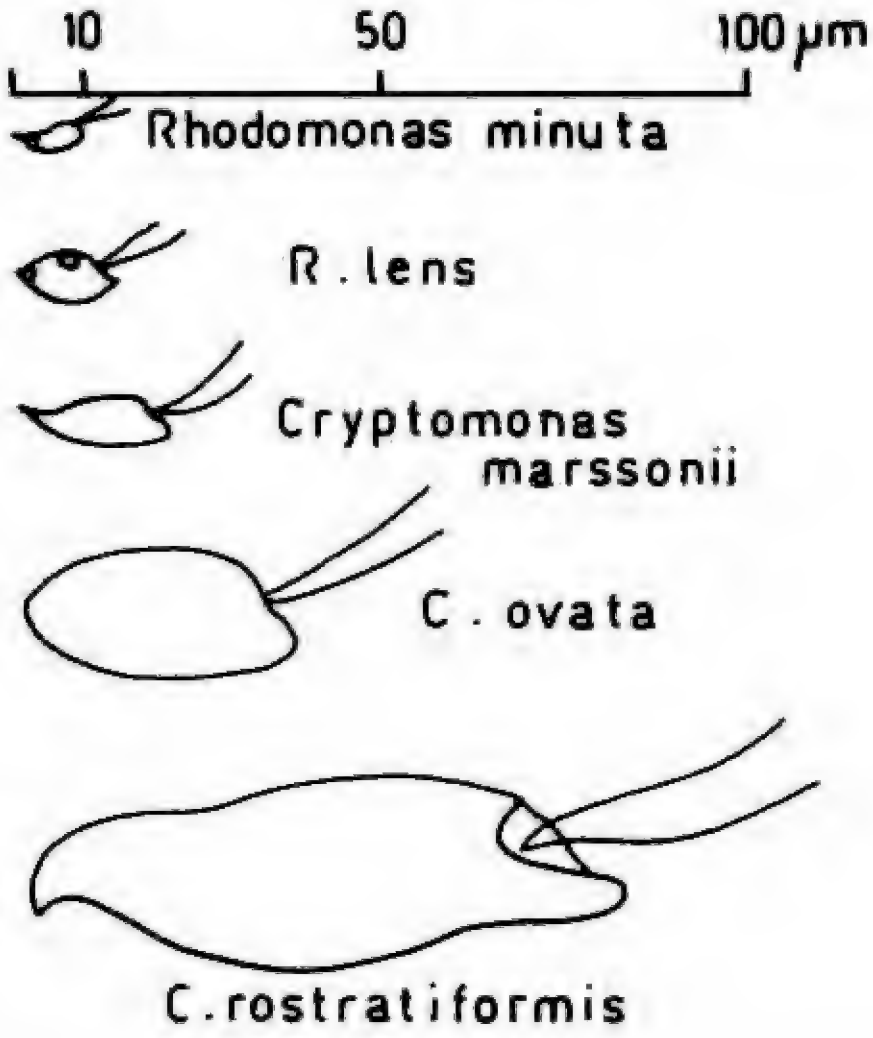

Figure 1
Cryptophyceae in Lake Constance.

Growth experiments were performed with natural phytoplankton enclosed in 2-liter bottles exposed at different depths, which were adjusted according to the water transparency of the respective phase of planktonic development. In order to avoid growth limitation by nutrient deficiency or by approach towards carrying capacity, epilimnetic samples were diluted at a ratio of 1:10 by nutrient-rich, phytoplankton-poor hypolimnetic water. Zooplankton was removed by filtration through a 100-µm mesh-size screen. Subsamples for cell counts were taken at the beginning and at the end of the exposure time. Making allowance for minor differences in temperature, all environmental factors except light intensities were identical between the different bottles within one experiment. It is known from earlier experiments (Heaney and Sommer 1984) that Cryptophyceae do not achieve their open-water growth rates when enclosed in bottles. To factor out this detrimental "bottle effect" in further analysis, an internal standardization was done for each species, assuming that the bottle effect was not depth specific. First the (observed) growth rate for each species was calculated:

$$k = \frac{\log_e N_2 - \log_e N_1}{t_2 - t_1} \tag{1}$$

Where t is the time in days, N is the number of cells at time t, and k is the specific rate of increase in units of d^{-1}. Then the highest value of k for each species within one experiment was k_{max} and all other growth rates were expressed as k_{rel} (relative

growth rate):

$$k_{rel} = \frac{k}{k_{max}} \tag{2}$$

Values for daily irradiance were obtained from "Deutscher Wetterdienst" (German Weather Service) and the data for the vertical attenuation coefficient (ϵ) of the lake water were kindly supplied by Prof. M. Tilzer. Algal cells were counted under the inverted microscope. Counting of at least 400 individuals per species and per sample gave a counting precision of ± 10% (Lund, Kipling and Le Cren 1958).

RESULTS

Migration Experiments

The migration experiments were performed on three occasions which provided large differences in water transparency: at the height of the spring bloom (28 May, $\epsilon = 0.85\ m^{-1}$), near the end of the spring bloom (3 June, $\epsilon = 0.66\ m^{-1}$), and in the middle of the clear water phase (15 June, $\epsilon = 0.26\ m^{-1}$). Four species produced a clear pattern of stratification, thus indicating vertical migration. Only *Cryptomonas ovata* remained randomly distributed until the end of the exposures (Fig 2). Usually in one of the tubes vertical migration was stopped by the ceiling or by the bottom of the tube ("truncation effect"). Hence, only tubes where the mode of the depth distribution was not at one of the ends were considered.

In one case (*Cryptomonas rostratiformis* on 15 June) depth distribution was both truncated by the bottom of the upper and by the ceiling of the lower tube. Here, data from both tubes were pooled and 2 m was considered modal depth. Both with respect to modal depth and to median depth, the rank order among the migrating species was identical between all experiments (Table 1): *Cryptomonas marssonii* (shallowest)—*C. rostratiformis*—*Rhodomonas minuta*—*R. lens* (deepest). Between the first three there was considerable overlap, whereas *R. lens* was always clearly separated from the others.

Growth Experiments

Growth experiments were performed at the height of the spring bloom (26 to 31 May, average ϵ for the exposure time $0.80\ m^{-1}$), during the clear water phase (7 to 12 June, $\bar{\epsilon} = 0.25\ m^{-1}$), and during the first algal growth phase in summer (4 to 8 July, $\bar{\epsilon} = 0.55\ m^{-1}$). As expected, growth rates in bottles were rather low (k_{max} for *Rhodomonas minuta* = $0.43\ d^{-1}$, *Rhodomonas lens* = $0.37\ d^{-1}$, *Cryptomonas marssonii* = $0.35\ d^{-1}$, *Cryptomonas ovata* = $0.35\ d^{-1}$, *Cryptomonas rostratiformis* = $0.32\ d^{-1}$, *Asterionella formosa* = $0.42\ d^{-1}$). The migrating species achieved positive growth rates only in very restricted depth ranges. The rank order of depth optima was the same as in the migration experiments (Fig 3). *Cryptomonas ovata* had a slightly wider depth range of positive growth than the other Cryptophyceae. For sake of comparison also a nonflagellated alga *Asterionella*

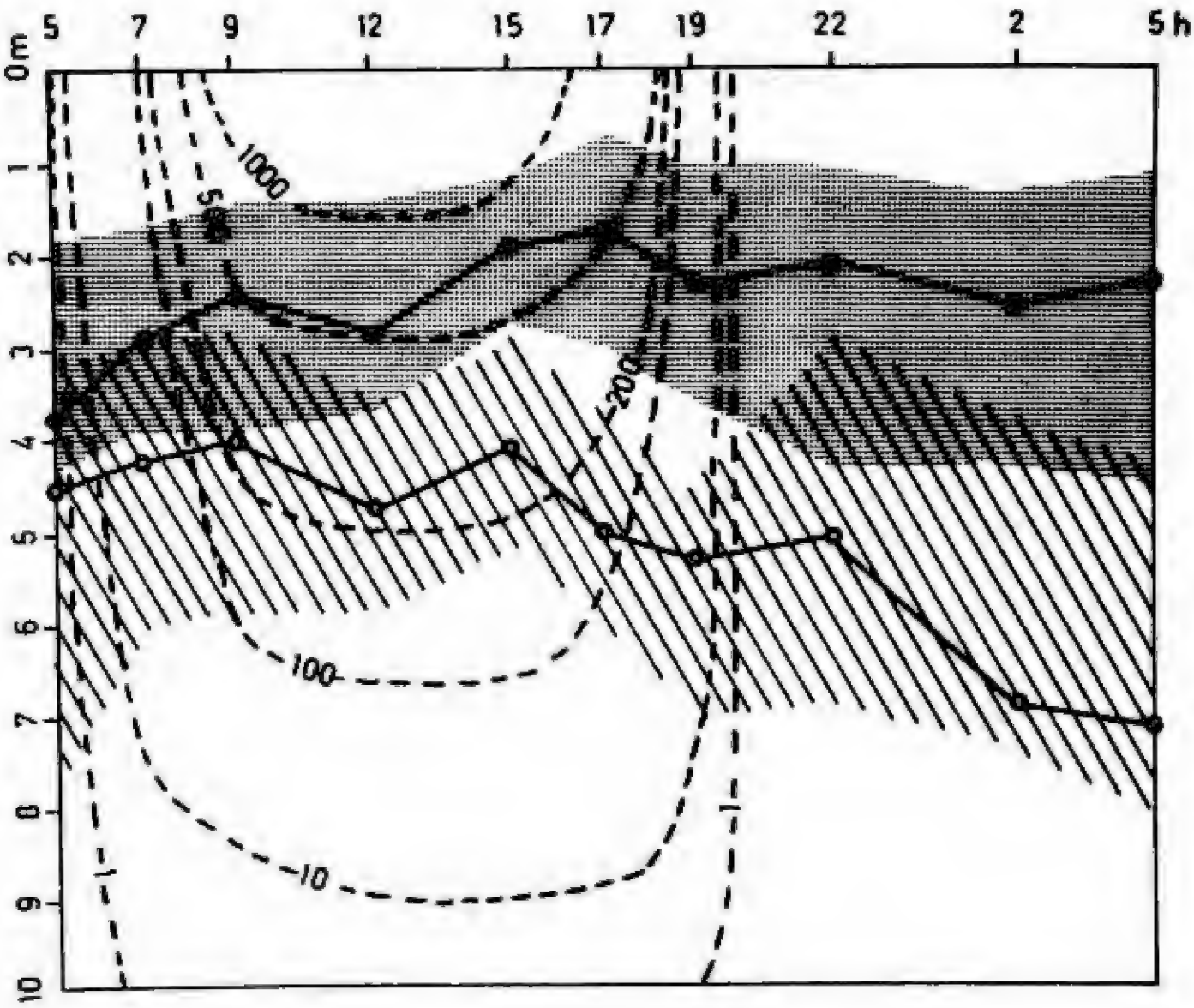

Figure 2

Migration experiments (1983). Distribution of algae (CM: ***Cryptomonas marssonii***, CR: *C. rostratiformis*, RM: ***Rhodomonas minuta***, RL: *R. lens*, CO: *C. ovata*) at the end of exposures inside the tube. Tubes where migration was significant and not truncated are indicated by hatching. Black: interquartile zone of depth distribution, broken line: median depth, numbers: % of surface light at median depth.

formosa Hass. was studied. It achieved positive growth rates in all bottles except one and had near to maximum growth rates in a wide depth range. Depths were converted to light intensities by using the average surface irradiance data (continuous record) and the average vertical attenuation coefficients (logarithmic interpolation) for the exposure periods. The dependence of the relative growth rate on light intensity (Fig 4) varied slightly within each species. All species exhibited lowest light requirements during the spring bloom experiment (lowest water transparency) and highest light requirements during the clear water phase (highest water transparency).

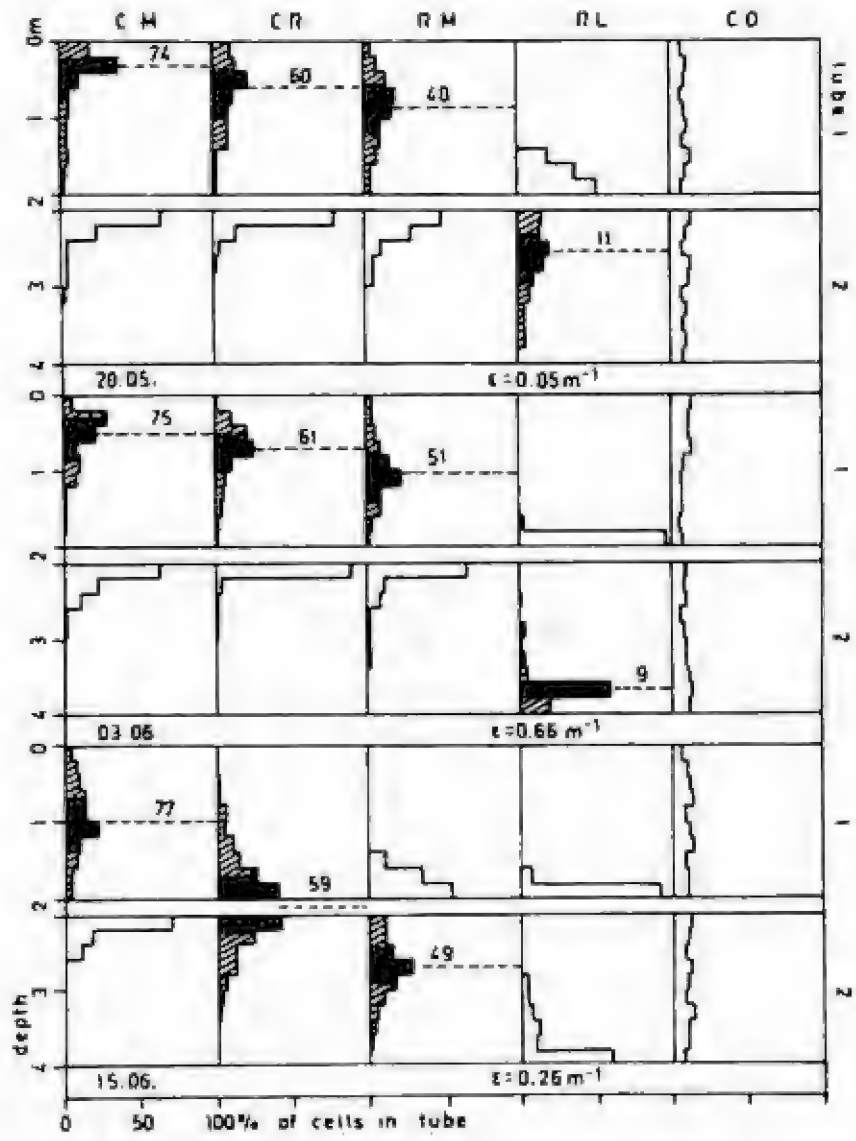

Figure 3

Growth experiments (1983). Algal abbreviations as in Figure 2, AF: ***Asterionella formosa***. Relative growth rate (k_{rel}) plotted against depth. Attenuation coefficients (ϵ) and surface light intensities (I_0) are mean values for the exposure period.

DISCUSSION

The main adaptive advantages of vertical migration of phytoflagellates may be concentration near the depth of optimum light (Tilzer 1973, Heaney and Talling 1980), access to nutrient reserves in deeper water layers (Illmavirta, in press) or a combination of both (Heaney and Eppley 1981). In Lake Constance, Cryptophyceae only thrive when nutrients in the entire euphotic zone are available at probably saturating concentrations ($PO_4 - P > 10\ \mu g \cdot l^{-1}$, $NO_3 - N > 300\ \mu g \cdot l^{-1}$). In the growth experiments reported here, nutrients were even increased beyond this level by addition of hypolimnetic water. In the example reported here, adjustment of the vertical position according to the light gradient seems to be the predominant adaptive significance of migration. This conclusion is substantiated by the fact that the rank orders of depth distribution and of growth response to light were identical for the four migrating species. The separation of ***Rhodomonas lens*** as a shade-adapted alga is beyond any doubt and agrees with earlier observations (Sommer 1982). Between ***Cryptomonas marssonii***, ***Cryptomonas rostratiformis*** and ***Rhodomonas minuta*** there remained some overlap both in depth distribution and in light requirements.

Table 1

Migration experiments: depth distribution of migrating Cryptophyceae at the end of exposure in relation to light climate. The first number gives the proportion of surface light(%), the second number, the average afternoon (1200 to 1700 h) light intensity at that depth ($J \cdot cm^{-2} \cdot h^{-1}$).

Species	Date	Light intensity at: mode depth		median depth		upper quartile		lower quartile	
Cryptomonas marssonii	5/28	77	196	74	188	82	208	55	135
	6/3	82	220	73	196	81	217	58	156
	6/15	75	153	77	157	84	171	71	145
Cryptomonas rostratiformis	5/28	65	165	60	152	72	183	43	109
	6/3	63	169	60	161	71	190	51	137
	6/15	59	120	59	120	64	131	55	112
Rhodomonas minuta	5/28	55	140	49	124	60	152	36	91
	6/3	48	129	51	137	61	164	40	107
	6/15	50	102	49	100	53	108	47	96
Rhodomonas lens	5/28	12	30	11	28	13	33	8	20
	6/3	8.7	23	8.7	23	9.3	25	8.2	22
	6/15	no results because of truncation effect							

Nevertheless, their rank order was reproducible in all experiments. The ecological differentiation with respect to light between those series seems to be stable. The observed absence of vertical migration in *Cryptomonas ovata* might be compensated by a flatter shape of the growth-light curve, although *C. ovata* is not as much a generalist with respect to light as *Asterionella formosa*. There is also some possibility that several genotypes with different behavior are lumped together under *C. ovata*, which is morphologically not as uniform in Lake Constance as the other species.

Differential light requirements of the Lake Constance Cryptophyceae are important in the separation of their ecological niches in terms of their time and light optima (Fig 5). Figure 5 is a two-dimensional representation in which the time optima (x-axis) are defined as successional stages (Sommer 1981) during which the relative contribution of the respective species to total algal biomass (p_i) exceeds its annual average ($\bar{p}$) plus the standard deviation

$$p > \bar{p} + s \tag{3}$$

Period 1 represents the small growth pulses during early spring before the onset of stable stratification. Period 2 is the spring bloom, which starts with the stabilization of stratification in April/May. Period 3 represents the clear water phase, during which

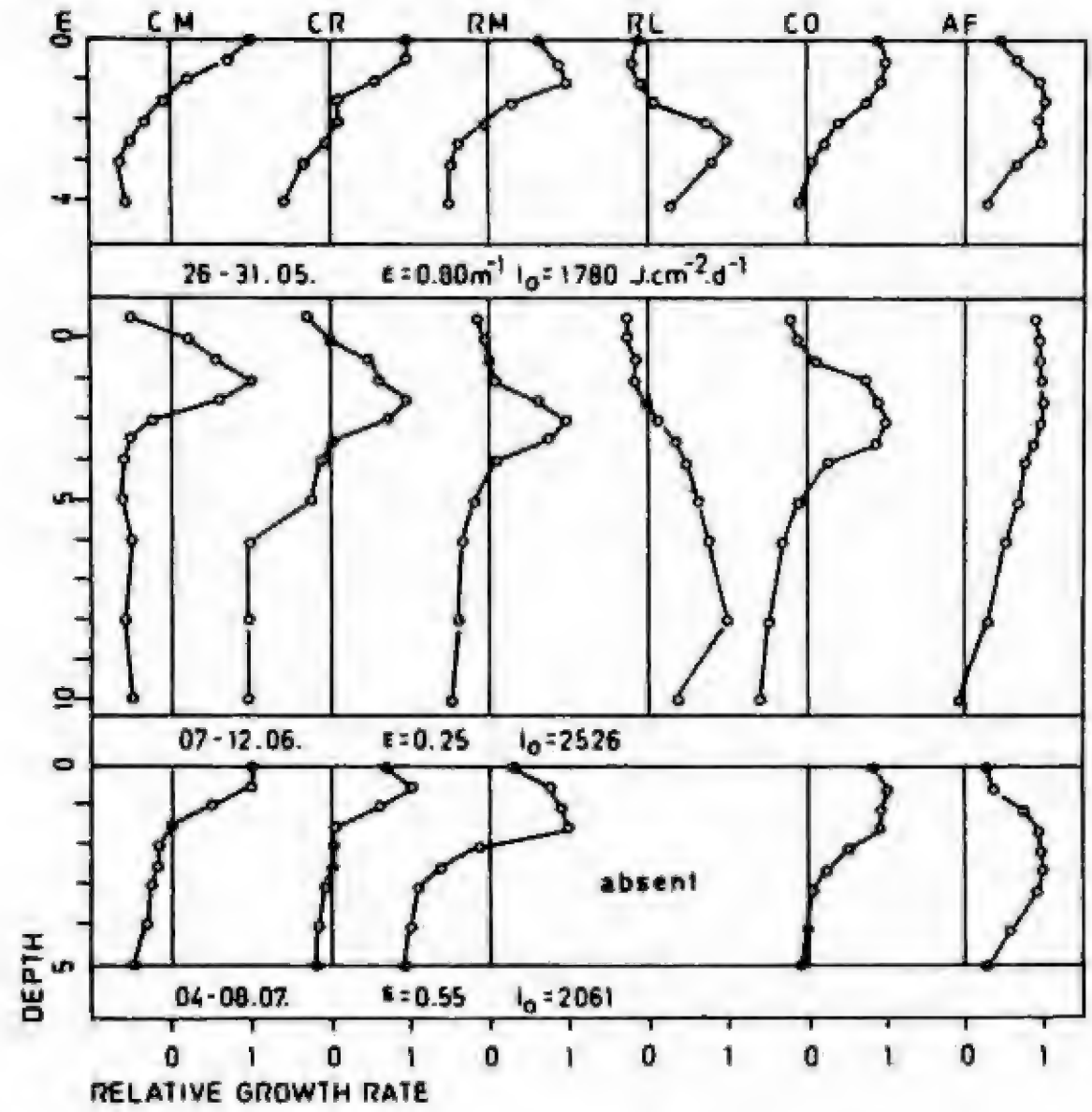

Figure 4

Growth experiments (1983). Relative growth rates plotted against average daily light intensity of exposure period. Full circles: 26−31 May. Open circles: 7−12 June. x: 4−8 July.

excessive grazing leads to extremely low phytoplankton densities (Lampert and Schober 1978). Period 4 is the first summer growth phase after the end of the clear water phase, during which ambient nutrient concentrations are still nonlimiting. The light optimum (y-axis) is derived from the growth experiments. Any light intensity at which at least in one experiment a relative growth rate of 0.8 was exceeded was considered to belong to the light optimum. Along both axes there is a considerable degree of overlap. If projected into a two-dimensional field, overlap between *Cryptomonas marssonii* and *C. rostratiformis* and between *C. rostratiformis* and *Rhodomonas minuta* is very much reduced, while *R. lens* shows no overlap with any other species. Only the two-dimensional optimum field of nonmigrating *C. ovata* overlaps to any significant extent with other species.

Among the vertically migrating Cryptophyceae in Lake Constance, migration seems to be a necessary compensation for specialized light requirements. Under calm hydrographic conditions these specific light optima are expressed by differential vertical distribution of algae which would have positive association indices among each other, if comparison were restricted to temporal distribution alone.

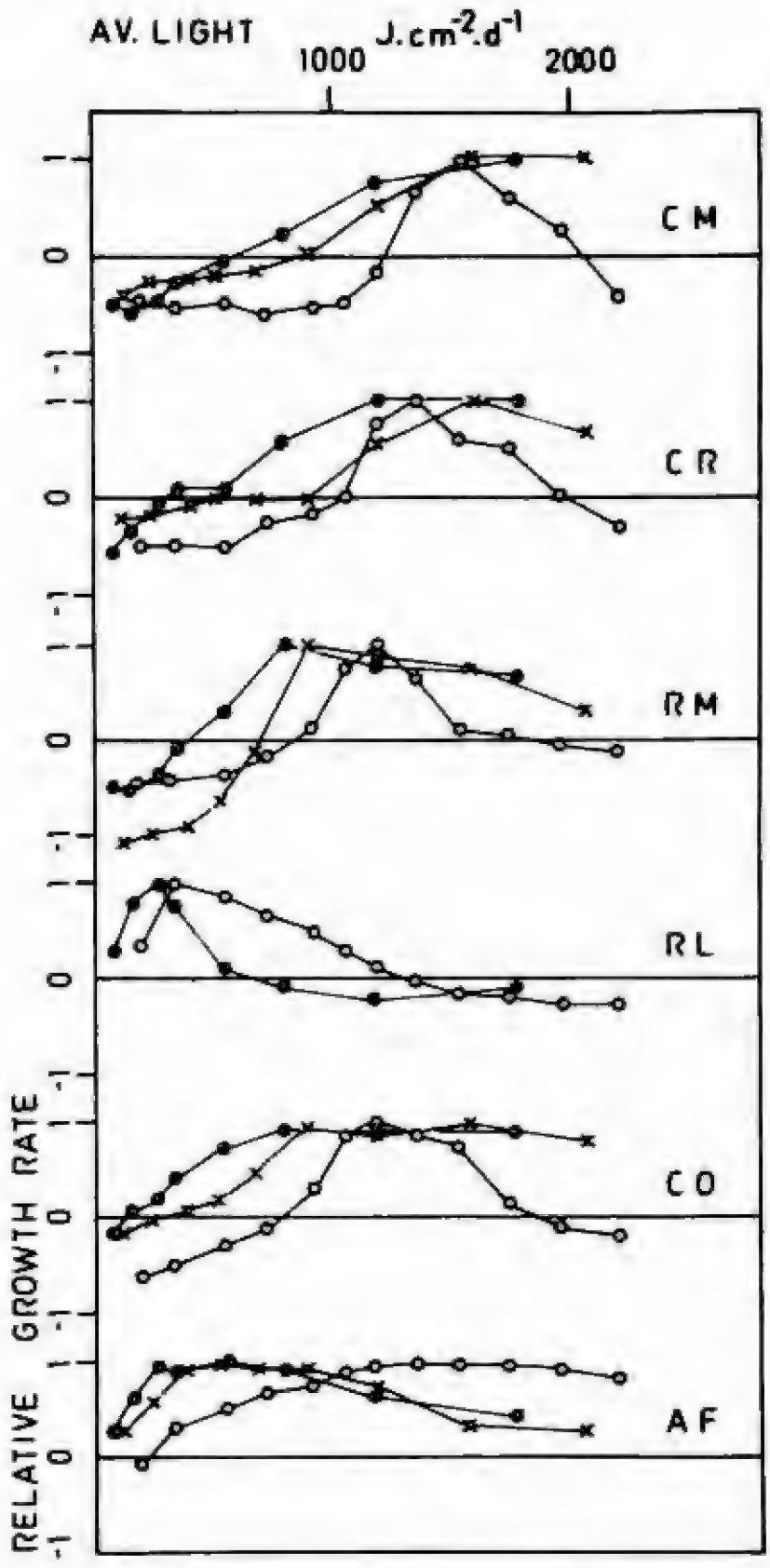

Figure 5

Ecological niches of Cryptophyceae with respect to light and time. Definition of time and light optima given in text. The migrating flagellates are represented by black bars and hatching, *Cryptomonas ovata* by shading.

In 1961 G.E. Hutchinson posed the "paradox of the plankton," questioning how a community without niches could be as diverse as the phytoplankton of natural lakes. Since that time an increasing number of ecological distinctions between algal species have been described, e.g. differential nutrient requirements (Tilman, Kilham and Kilham 1982) and differential predation by zooplankton (Porter 1973). Variation in migration as a consequence of differential light requirements may now be added to this list. Even if water movements will at times prevent flagellates from reaching their optimum depth, the combination of light fluctuations and of differences in light

requirements will lead to shifts in competitive advantage among these species, and competitive exclusion will not be reached.

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A SURVEY OF PROTOZOAN LABORATORY TEMPERATURE STUDIES APPLIED TO MARINE DINOFLAGELLATE BEHAVIOR FROM A FIELD PERSPECTIVE

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ABSTRACT

Iterative biophysical models that incorporate marine dinoflagellate behavior require detailed time-series information that encompasses the acclimated and acclimating responses of both swimming speed and orientation in order to be properly parameterized. At the present time a survey of the available information dealing with temperature effects on swimming behavior demonstrates that adequate time-series information is not available. This lack can be ameliorated through an application of available video technology to developing experimental systems that more closely represent the field situation. A nonlinear statistical analysis is also proposed that can be useful in distinguishing between the temperature versus swimming speed capabilities of different species. The application of these experimental tools and the eventual application of the results to biophysical models should provide new insights into how dinoflagellates utilize motility to their competitive advantage in response to environmental variability.

INTRODUCTION AND METHODS

The behavior of marine dinoflagellates from an ecological perspective is presently studied most intensively by sampling field populations or by using laboratory cultures in standing water columns of various sizes. Forward (1976) reviewed the field observations. Subsequent coastal records include Kiefer and Lasker (1975), Blasco (1978), Kamykowski (1980), Staker and Bruno (1980) and Cullen and Horrigan (1981). In addition, Tyler and Seliger (1981) provided an elegant estuarine study of a dinoflagellate population that was relatively restricted by land and currents. They demonstrated that the behavioral reactions of ***Prorocentrum mariae-lebouriae*** to temperature, salinity, light, nutrients and possibly other factors must be known in order to successfully interpret the observed distribution of this species in Chesapeake Bay. Unfortunately, restricted dinoflagellate populations are unlikely in open coastal

and oceanic waters. Various investigators used land-based water columns to obtain time-series behavioral measurements of dinoflagellate species from such relatively unrestricted areas. Eppley, Holm-Hansen and Strickland (1968) studied the effect of clouds and nutrient concentrations and Kamykowski and Zentara (1977) studied the effect of thermal stratification in large land-based columns (10 m high, 3 m diameter). Staker and Bruno (1980), Cullen and Horrigan (1981), Heaney and Eppley (1981) and Kamykowski (1981a) performed a range of experiments which considered temperature, salinity, light, and nutrient concentrations and used smaller columns generally less than 2 m high. All of these studies emphasized sequential biomass measurements to determine changing species distribution and assumed that the average cell follows the behavior suggested by the movement of the biomass peak in the water column.

One method of extending and generalizing these field and column observations is through biophysical models. Woods and Onken (1982), studied the effect of diurnally varying solar radiation and vertical circulation on primary production and dubbed one fruitful class of these models the Lagrangian ensemble approach. Kamykowski (e.g., 1981b) used a similar approach to simulate the interaction between dinoflagellate behavior and physiology and internal wave currents and thermocline motions. As these models are generally solved through iterative calculations over short time increments, the time-series details of dinoflagellate behavior and physiology are critical variables. The ideal biological subsystem model should respond to changing environmental conditions with realistic direction, intensity and time lag. The kind of information required to build such a biological subsystem model is accumulating for the photosynthetic response of dinoflagellates (Prézelin and Sweeney 1978) and for nutrient uptake (Cullen and Horrigan 1981, Harrison 1976). Though some pertinent information on dinoflagellate behavior is available, the required detail is lacking in the ecological literature due to the coarseness of the biomass techniques. Some of the requisite information is potentially available from the visual laboratory techniques developed for the study of protozoan motility per se (Pfau et al. 1983). Past applications of these techniques, however, have generally lacked appropriate field focus or statistical rigor. The present paper will review the available literature pertaining to dinoflagellate time-series responses of translational velocity to temperature changes. Moving from the simpler to the more complex, swimming speed studies will be emphasized, with some information provided on orientation effects. The latter must assume an equal position, after the temperature effects on swimming speed are better defined. Temperature is the chosen variable because dinoflagellates are known to cross temperature gradients within a certain range (Kamykowski 1981a) and because the field patterns predicted by models are most dramatic when the thermocline is crossed. Suggestions will then be offered for improving the data base.

PROTOZOAN OBSERVATIONAL LITERATURE

Reviews

Though the present focus is on the behavioral reactions of protozoa, and specifically marine dinoflagellates to temperature, a rich observational literature exists that considers a broad spectrum of environmental variables. This literature is extensively reviewed by Jahn and Bovee (1967) and more selectively reviewed with a focus on dinoflagellates by Levandowsky (in press). Holwill (1966) and Brennen and Winet (1977) provided additional information on temperature effects. The following discussion will first consider swimming speed in terms of acclimated and acclimating responses and then swimming orientation.

Temperature Acclimation Defined

Prosser (1964) provided a thoughtful discussion of physiological adaptation defined as any physiological property of an organism which favors survival in a specific environment. Of more immediate interest, acclimation refers to compensatory alterations in an organism during maintenance under laboratory conditions altered by one stressful parameter. An acclimated organism is therefore one that is in physiological equilibrium with respect to this environmental factor. Holwill (1966) and Brennen and Winet (1977) reviewed the swimming speed observations of a variety of flagellated or ciliated organisms including dinoflagellates. Their survey assumes that the organisms are acclimated to the recorded temperature, the sole environmental variable listed in their tables. The following section describes the acclimation of protozoan motility to temperature.

The Protozoan Acclimation Process

Kinne (1964) considered how aquatic crustaceans acclimate various physiological processes to the full range of environmental temperatures and compared rates obtained in a gradually changing temperature regime to rates obtained after acclimation to various constant temperatures. The rates obtained under gradually changing temperatures generally are less than acclimated rates under conditions of slowly rising temperatures and are greater than adapted rates under conditions of slowly declining temperatures. These guidelines appear applicable to protozoa based on the available information discussed below.

Hopkins (1937) provided the most complete study of the acclimation of protozoan motility to temperature using the marine amoeba ***Flabellula mira*** Schaeffer. His general conclusions were:

1. Locomotion rate increases with temperature to a maximum and then decreases rapidly at higher temperature.
2. Adjustment to a decrease in temperature seems slower than adjustment to an increase in temperature.

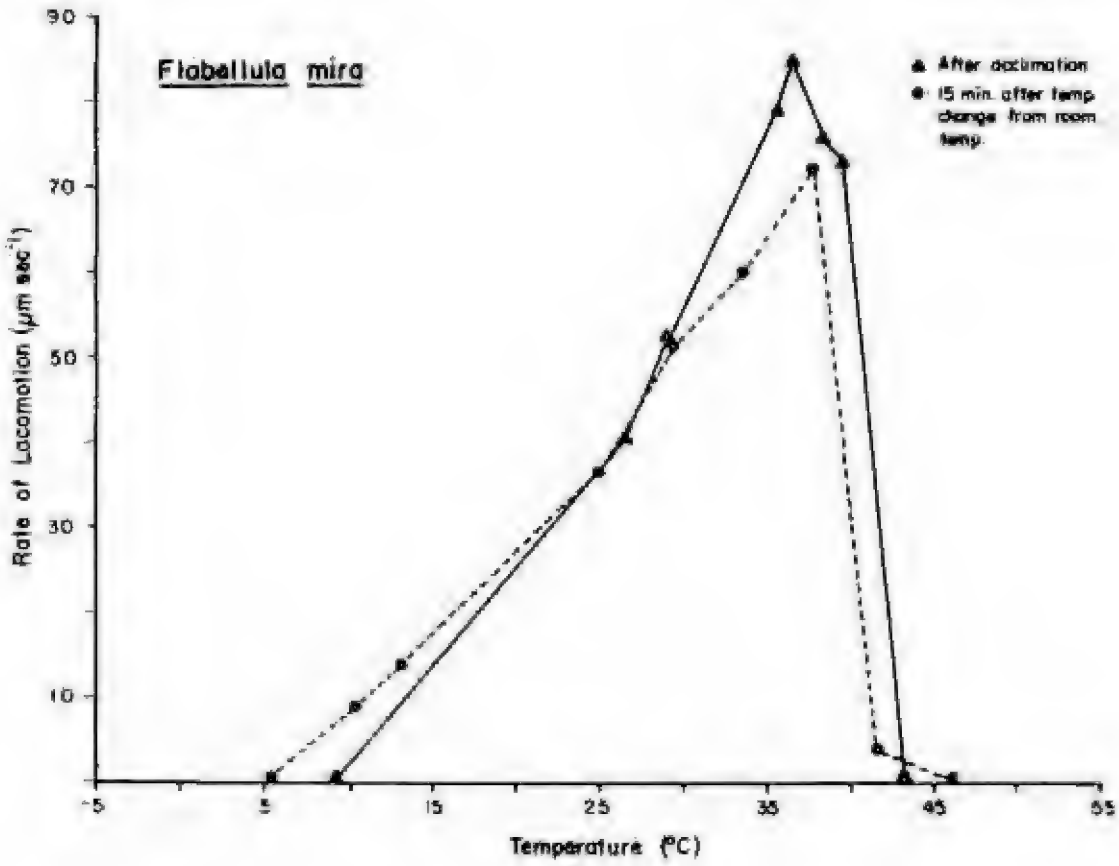

Figure 1

The rate of locomotion of *Flabellula mira* as measured 15 min after transfer from room temperature to higher or lower temperatures and compared to that after acclimation (several hours) to the new temperature. (After Hopkins (1937).)

3. Sudden increases in temperature cause oscillations in locomotion responses; the smaller the increase, the fewer the increases and decreases in a given time.
4. Sudden decreases in temperature cause instantaneous decreases in locomotion rate, and this rate continues to decrease gradually for several hours; up to seven hours may be required for cells to cease moving after a change to a lethal low temperature.
5. Gradual temperature changes ($5°C \cdot h^{-1}$) do not allow full acclimation; at temperatures lower than the acclimated temperature, the rate is lower after acclimation to the new temperature. At temperatures higher than the acclimated temperature, the rate is usually higher after acclimation (Fig 1).
6. The instantaneous rate of locomotion at a given temperature depends upon the temperature to which the amoeba has previously been acclimated.

Shortess (1942) observed the ciliate *Perinema trichophorum* over 2-h periods, reporting that:

1. The rate of locomotion increases with temperature to a maximum and then decreases rapidly at higher temperatures.
2. The rate of locomotion in *Perinema* acclimated to an intermediate temperature varies little with time when exposed to constant temperatures which range from 14°C to 36°C but decreases rapidly at temperatures higher than 36°C (Fig 2).
3. The instantaneous rate of locomotion at any given temperature depends upon the acclimation temperature.

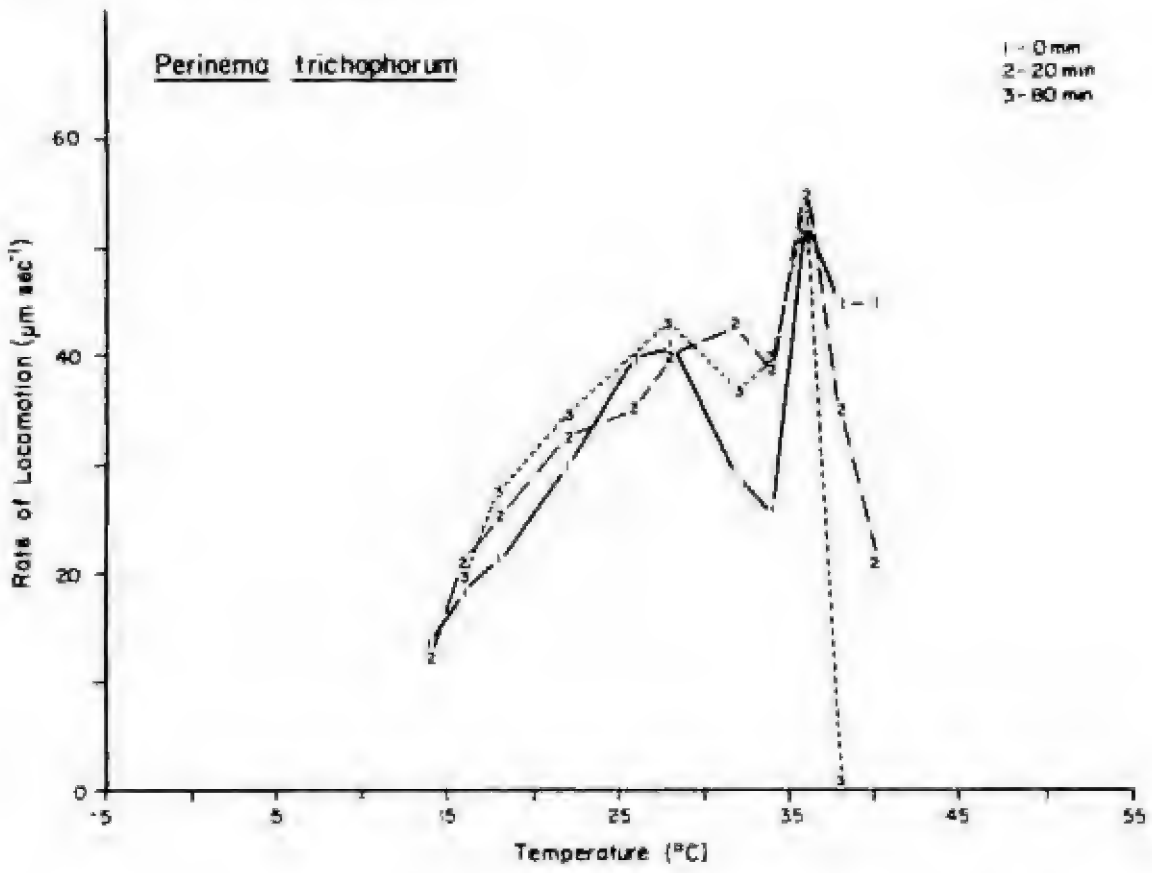

Figure 2

The rate of locomotion of ***Perinema trichophorum*** measured 0, 20 and 80 min after transfer from room temperature to higher or lower temperatures. (After Shortess (1942).)

4. Light of moderate intensity has no appreciable effect on the locomotion at any temperature, but very intense light causes a considerable increase in the rate of locomotion at temperatures below 14°C and a marked decrease at temperatures above 14°C.

Differences between the observations of Shortess (1947) and those of Hopkins (1937) may be related to differences in mode of locomotion (ciliary vs. amoeboid movement). Another possibility is that the discrepancy in the results of these two workers is due to the difference in the duration of their experiments.

Two papers discuss the swimming speed response of flagellated protozoans. Based on studies over 2-hour periods, Lee (1954) reported on ***Euglena gracilis*** and ***Chilomonas paramecium***:

1. Maximum swimming speed occurs at intermediate temperatures (25−30°C) with very sharp decreases at higher or lower temperatures.
2. These species exhibit no temporal change in the swimming rate when organisms are held at constant temperature levels at 5° intervals between 5−40°C.

The lack of a high temperature effect may be due to the few observations obtained above 30°C. The otherwise general agreement of these results with those of Shortess (1942) probably results from similar experimental duration. Using innovative measurement methods, Hand, Collard and Davenport (1965) studied the temperature dependence of the swimming speed of two dinoflagellates ***Gonyaulax*** sp. and *Gyrodinium* sp. and found:

1. Cells exposed to a rapid temperature decline (20° to 8°C in 10 min) maintain motility to 12°C, and cells kept at 8°C for 12 hours do not recover motility. Cells exposed to a rapid temperature increase (20° to 34°C in 20 min) lose motility at 28°C, but cells maintained at this temperature recover motility in about an hour.
2. If ***Gonyaulax (Gyrodinium)*** undergoes a gradual increase in temperature ($2°C \cdot 30\ min^{-1}$), it maintains motility to 34°C (38°C); cells maintained at 34°C (38°C) for 12 hours never recover motility. Under gradually decreasing temperature, cells maintain motility to 8°C (4°C) (Fig 3).
3. Both species maintain uniform velocity throughout a wide temperature range.

According to the results of Hopkins (1937), these experiments also may lack sufficient duration to allow full acclimation at the various temperatures at which measurements were made. The relationships presented in Figure 3 may therefore be a complex function of incomplete acclimation.

As previously mentioned, Hopkins (1937) observed in an amoeba that sudden increases in temperature cause oscillatory locomotion responses and that sudden decreases in temperature cause instantaneous decreases in locomotion rate which continue to gradually decrease for several hours. The swimming speed changes occurring in the first few minutes of exposure to a new temperature were studied in ***Paramecium*** (Tawada and Oosawa 1972) and ***Chlamydomonas*** (Majima and Oosawa 1975). ***Paramecium*** exhibits an initial swimming speed increase to temperature changes greater than ± 1°C and then an exponential decrease with time (ca. 1 min) to a new steady rate. ***Chlamydomonas*** responds to a sudden temperature increase (decrease) by increasing (decreasing) its swimming speed. The high (low) velocity is maintained for few minutes, the velocity then decreases (increases) in a few minutes. These observations, telescoping the first few minutes of a temperature change, may help in the formulation of a conceptual model of ecological responses to temperature gradients, but such detailed behavior may not significantly contribute to integrated interactions that occur over a day.

Taken together, these protozoan references suggest that dinoflagellate swimming speed might respond to temperature change over several time scales extending from instantaneous reactions to additional adjustments toward acclimation that require several hours (at present, this is speculation) especially at temperatures below the acclimation temperature. As the natural exposure of a given dinoflagellate species to altered temperatures may range from minutes to hours in a diurnal vertical migration, depending on the depth range traversed and on the thermocline depth, a comparable spectrum of information on swimming capabilities and acclimation is required to modulate behavioral rates in interactive biophysical models. This necessary information cannot presently be generalized either for individual ecologically significant species nor even for the dinoflagellates as a class.

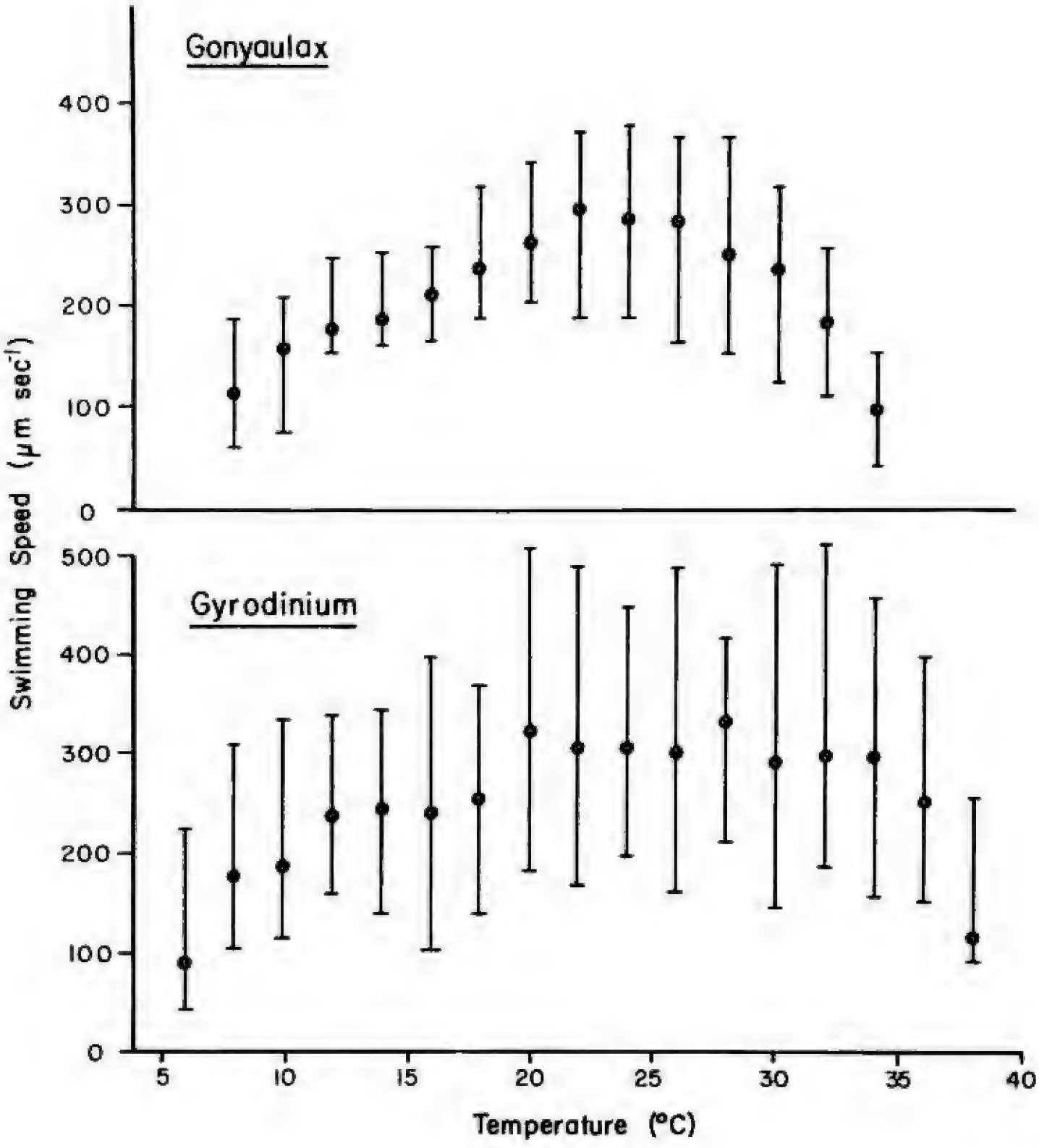

Figure 3

The rate of locomotion (linear swimming speed) of *Gonyaulax* and *Gyrodinium* acclimated to 20°C at lower and higher temperatures encountered at a rate of 2°C per 30 min. (After Hand et al. (1965).)

Orientation

Velocity is a vector. Though the present discussion emphasizes temperature effects on protozoan swimming speed, temperature can also affect the swimming orientation of protozoans, including perhaps dinoflagellates. Nakaoka & Oosawa (1977) examined a strain of ***Paramecium caudatum*** which exhibited temperature-sensitive differences in the frequency of directional changes. In a survey of ***Paramecium***, most strains demonstrated their temperature sensitive behavior in this way. Nultsch (1974) reported thermotaxis, orientation of motile microorganisms in a given temperature gradient, in several classes of motile algae but did not list dinoflagellates. Kamykowski (1981) showed (Table 1) that different species of dinoflagellates exhibit different temperature thresholds for altered behavior. He observed that the absolute temperatures seemed more significant than the actual temperature gradient. Even this preliminary survey demonstrates that temperature apparently acts as a modifying factor on the behavior of dinoflagellates which are responding to other environmental variables. The dominant cues appear to be light (phototaxis) and gravity (geotaxis) (e.g., Eppley et al. 1968, Wilson 1975, Cullen and Horrigan 1981). In order to modulate behavioral orientation in interactive biophysical models, additional information is required on the effects of temperature and other factors on dinoflagellate responses to light and gravity.

A SUGGESTED LABORATORY PROGRAM

Prelude

A coherent, multifaceted, statistically rigorous experimental approach is required in order to generate the information on behavior-induced rates for interactive biophysical models. An initial attempt at such an approach is presented below which emphasizes temperature effects and is based on different applications of a video camera system. Several different combinations of hardware and software which are suitable for this purpose are available commercially. One such instrument array includes a microscope, light source, video camera, video screen, video stopwatch, time lapse recorder, and video caliper (Fig 4). This system allows a straightforward measurement of swimming speed and direction. More advanced systems are already available as described in Pfau et al. (1983) and by Buskey (1983) but the present system provides a relatively inexpensive though more laborious alternative. The different applications refer to three experimental designs: (1) the temperature gradient plate, (2) the water-jacketed cuvette, and (3) the two-layer, water-jacketed column used with parallel water-jacketed cuvettes. In addition, the data derived from some of these experiments can be analyzed by a robust nonlinear statistical analysis. These experimental designs and statistics will be discussed in more detail.

Table 1

Summary of ascent patterns for a dinoflagellate species under variable environmental conditions in a 2 m temperature stratified water column (after Kamykowski 1981a).

Organism	Salinity (ppt)	Bottom temperature	Top temperature	Ascent summary
Cachonina niei	36	14°C	25°C	Strong aggregation at surface
		10°C	25°C	Weak aggregation above thermocline
		14°C	25°C	Strong aggregation at surface
	27	15°C	23°C	Diffuse through column
		7.5°C	25°C	Diffuse through column
Ceratium furca	27	20°C	27°C	Weak aggregation in upper layer
Gymnodinium splendens	27	17°C	24°C	Strong aggragation at surface
Prorocentrum micans	27	16°C	25°C	Strong aggregation at surface

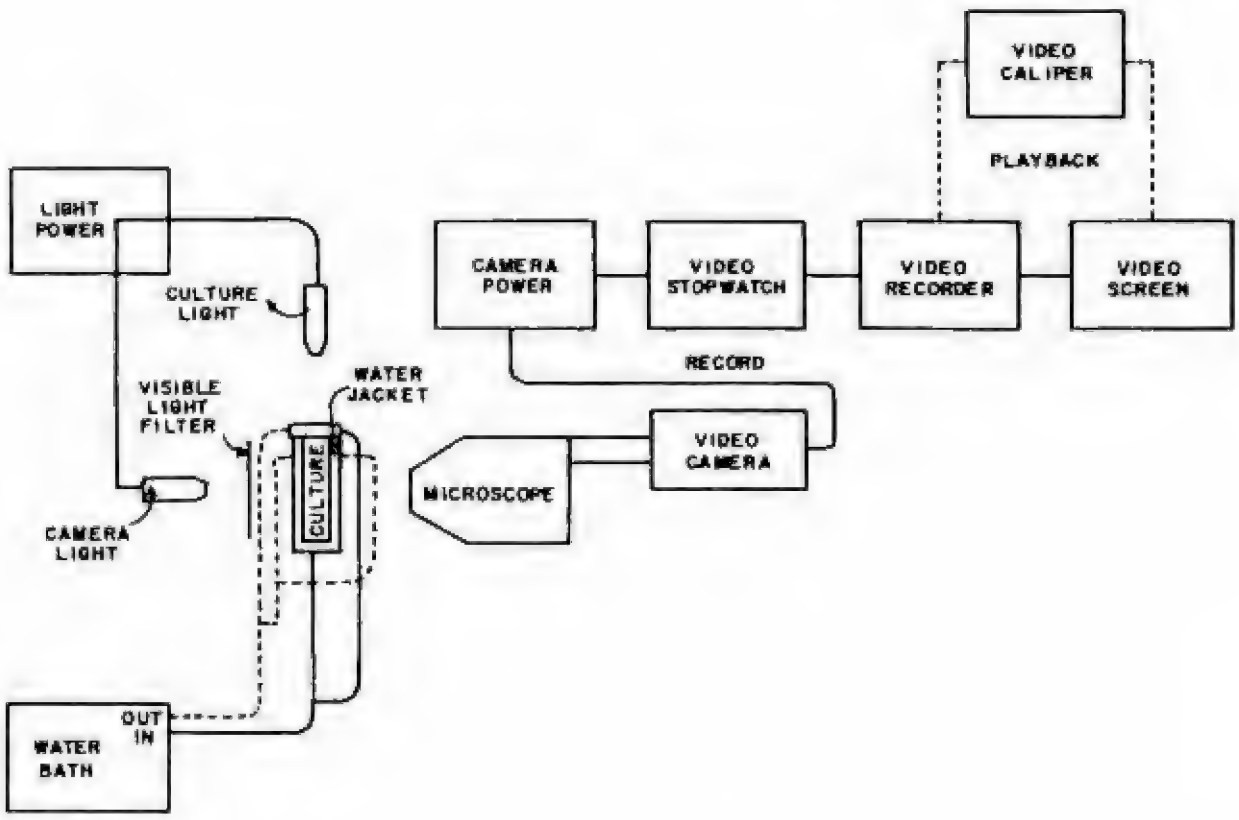

Figure 4

A schematic diagram of one workable array of video equipment that can be used to examine dinoflagellate swimming speed and orientation.

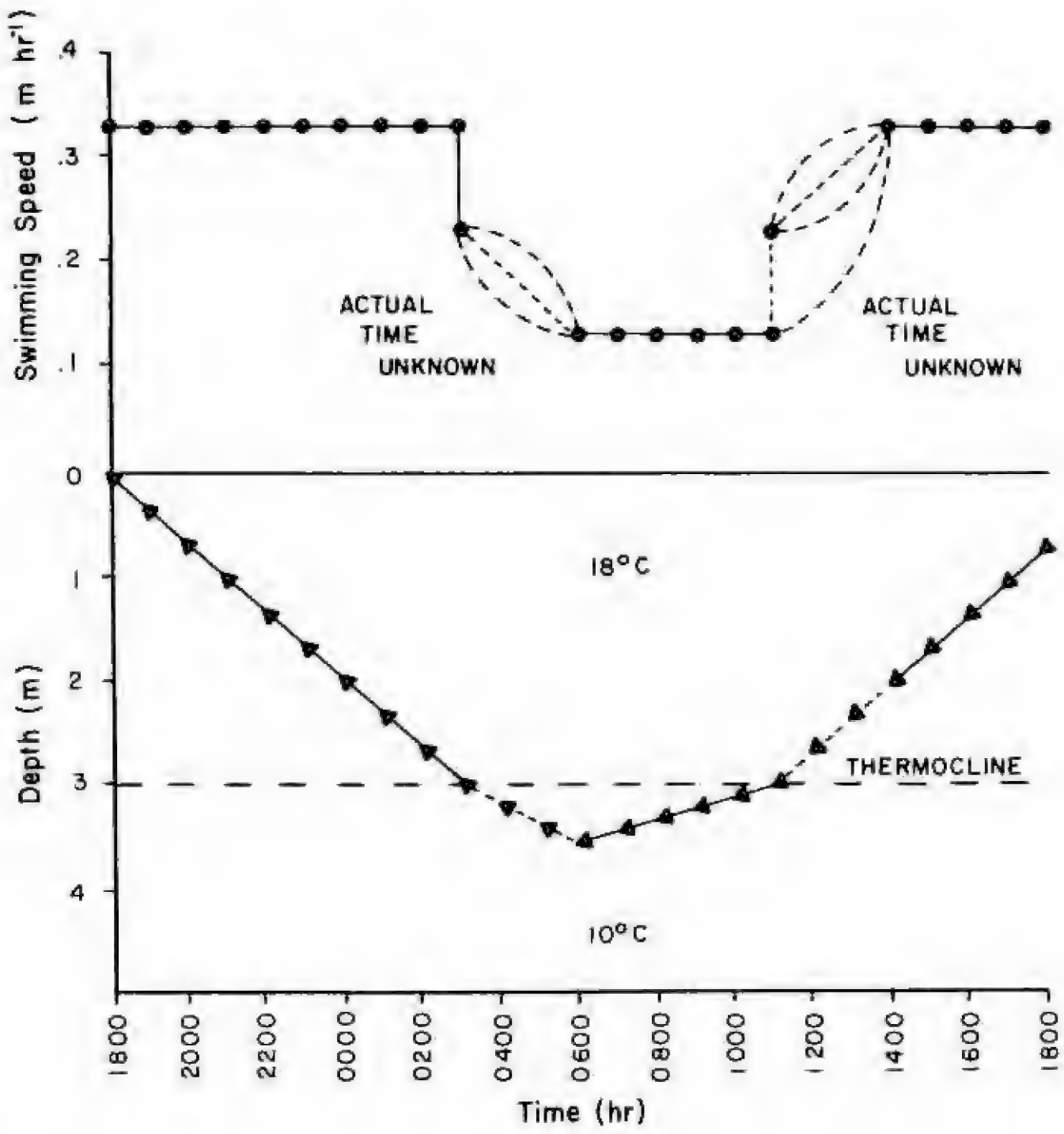

Figure 5

A conceptual view of how time lagged acclimation may affect dinoflagellate environmental exposure in a thermally stratified water column.

Experimental Apparatus

Temperature Gradient Plate—Van Baalen and Edwards (1973) described a light-temperature gradient plate suitable for maintaining algal cultures. In the present application, the fluorescent bulbs are positioned 7 cm apart just above an aluminum block (61 × 61 cm) that provides a temperature gradient from 1°C to 35°C. The fluorescent bulb and the temperature gradient are perpendicular. Disposable 1-cm spectrophotometer cuvettes are the culture chambers. The microscope with attached video camera is supported on a ball-bearing frame that allows positioning the camera over any point on the aluminum block. The microscope gear provides the vertical motion that focuses the camera image as the bottom of the microscope moves between the fluorescent bulbs. The long wavelength, spectrally filtered light (> 600 nm) for

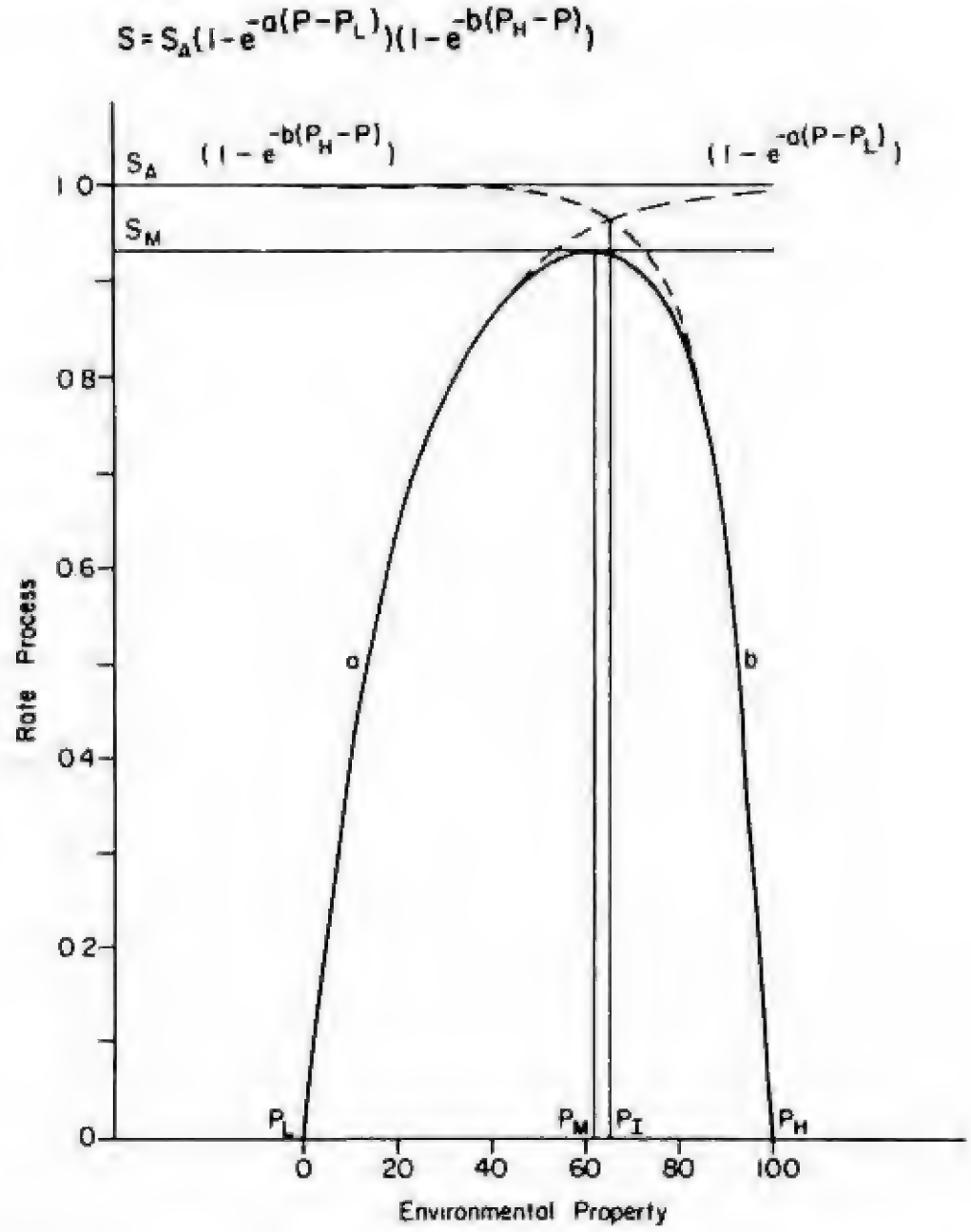

Figure 6

A generalized descriptive plot showing the character of a new empirical function that can be used to fit the relationship between temperature and swimming speed. The dashed lines at the top of the curve continue the trends of the respective exponential parts of the equation. *P* substitutes for *T* in Equation 1.

the camera is reflected off the aluminum block through the cuvette. This apparatus allows the determination of the relationship between acclimated swimming speed and temperature for several species of dinoflagellates as the organisms maintained in enriched seawater medium survive under the described conditions for several days with no apparent loss of vigor.

Water-Jacketed Cuvette—In order to determine the time course of dinoflagellate swimming speed response to temperature change, a second system is used. A water-jacketed acrylic cuvette (2.5 × 0.7 × 2.5 cm) is mounted on a screw rack resting on a screw elevating table. The cuvette can be moved through a plane. The microscope with attached video camera is mounted horizontally and the microscope gear provides motion along the third axis. Organism swimming speed can be recorded continuously as the temperature conditions are manipulated. This apparatus will help to determine the appropriate relationships in Figure 5, a conceptual view of how acclimation

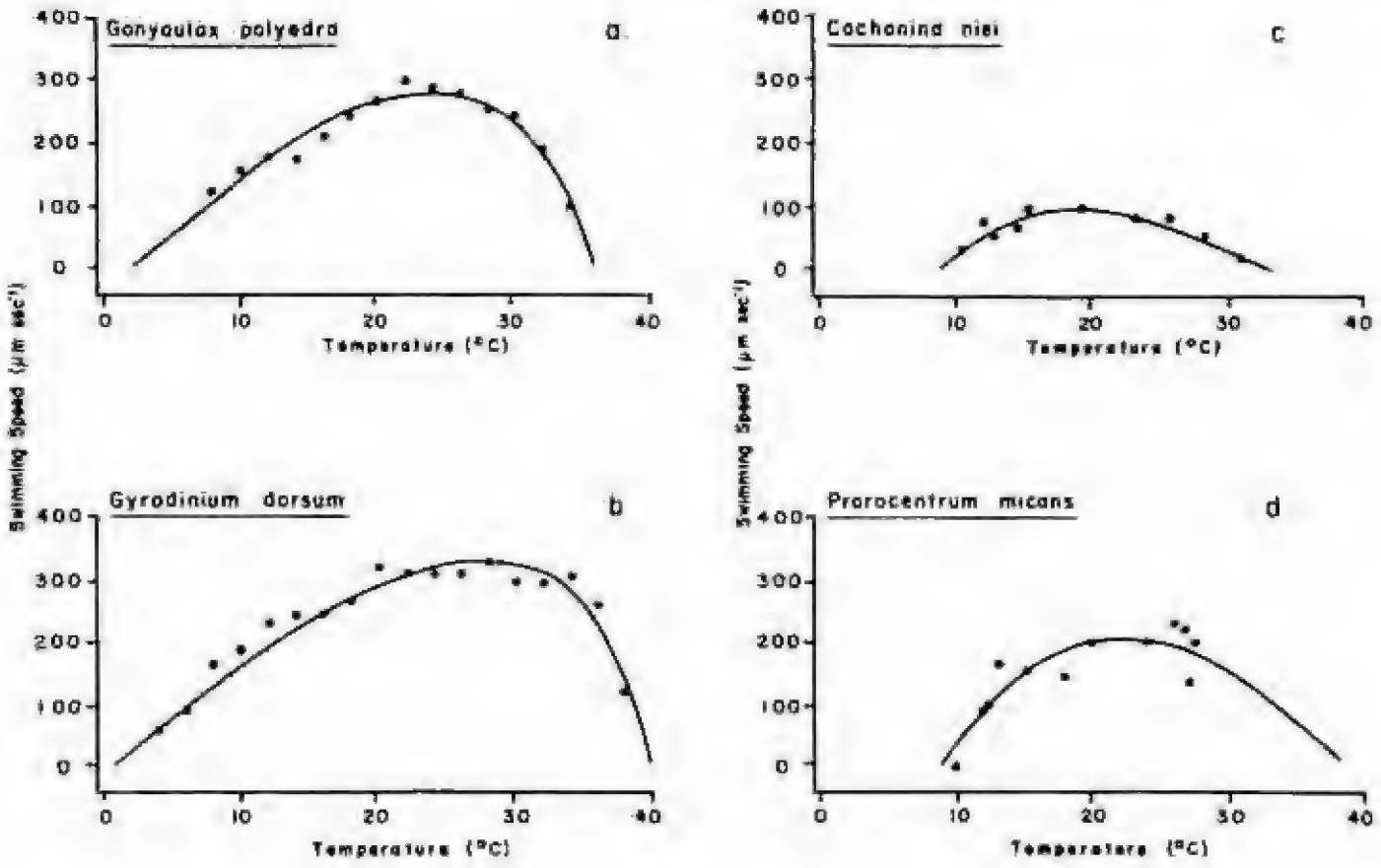

Figure 7

Plots of temperature (°C) versus mean swimming speed ($\mu m \cdot sec^{-1}$) for four species of dinoflagellates. The data in 10a and 10b are adapted from Hand et al.(1965); the data in 10c and 10d are original. The curved lines represent the fit of Equation 1 to the data.

processes may affect dinoflagellate interactions with physical regimes. It will also contribute information on the effects of temperature changes on cell orientation.

Two-Layer, Water Jacketed Column—The previous methods force the exposure of the organisms to different temperatures. The water-jacketed column allows the organisms to select their own positions in a temperature-stratified water column of enriched seawater medium. The unique aspect of this water column is that the six sampling posts, 3 in each layer, are paralleled by 2 sets of 3 water-jacketed cuvettes. One set of 3 cuvettes is maintained at the temperature of the upper layer of the water column and the other set of 3 cuvettes is maintained at the temperature of the lower layer of the water column. This arrangement allows the application of the video system as a measuring device applied to samples drawn from the water column. These measurements provide a visual parallel to the biomass fluxes in the water column that can be measured by standard means. This design can potentially provide information on the statistics of cell motion within the biomass peak.

Table 2

Least squares fit to Equation 1 for temperature versus swimming speed plots for four dinoflagellate species.

Species	df[beta]	a[γ]	*b*	T_L[δ]	T_H[δ]	S_A	T_M[ε]	S_M[ψ]	Body Type	Approximate Length (μm)
		$°C^{-1}$	$°C^{-1}$	°C	°C	m h^{-1}	°C	μm s^{-1}(m h^{-1}))		
Cachonina niei	5	0.121 ±0.339	0.041 ±0.318	9.0 ±2.3	33.0 ±1.4	1.20 ±1.41	18.9	103(0.37) ±0.05	Dinokont Armored	13
Prorocentrum micans	7	0.201 ±0.395	0.201 ±2.833	9.0 ±1.4	38.0 ±110.3	0.80 ±1.09	23.5	200(0.72)[ω]	Desmokont Armored	42.5
Gonyaulax[α] *polyedra*	9	0.041 ±0.075	0.161 ±0.119	2.2 ±3.0	36.0 ±0.7	2.00 ±2.57	24.2	281(1.01) ±0.05	Dinokont Armored	48
Gyrodinium[α] *dorsum*	13	0.041 ±0.038	0.201 ±0.107	1.0 ±1.8	40.0 ±0.9	2.00 ±1.20	28.1	338(1.22) ±0.13	Dinokont Unarmored	72

α = Hand et al. (1965); acclimating

β = n − 5

γ = Est ± 1 s.d.

δ = Caution: often based on extrapolated relationship.

ε = Estimated by iteration.

ψ = See Appendix I for calculation of confidence limits.

ω = Confidence limits cannot be calculated due to limited data base.

Statistical Analysis

Obtaining swimming speed data from the temperature gradient plate for different species will allow interspecies comparisons. These comparisons require the definition of appropriate biological parameters and a method to determine statistical differences. Data derived from the temperature gradient plate can be fitted to the five-parameter expression:

$$S = S_A \left(1 - e^{-a\,(T - T_L)}\right)\left(1 - e^{-b\,(T_H - T)}\right) \qquad (1)$$

where S is the swimming speed at temperature T, S_A is the asymptotic swimming speed for the two exponential curves, a is the initial slope, T_L is the low temperature at which swimming stops, b is the final slope, and T_H is the high temperature at which swimming stops (Fig 6). These five parameters (S_A , a, T_L , b, T_H) are provided with statistical confidence limits by the nonlinear curve fitting procedure in the Statistical Analysis System (SAS, 1982) procedure PROC NLIN. In addition, confidence limits can be computed for any predicted swimming speed at a given

temperature from Equation 1 using the partial derivatives of Equation 1 for each parameter and the variance-covariance matrix. Appendix 1 provides a model computation. The most obvious utility of this analysis centers on T_L , T_H and the estimate of S_M , the maximum swimming speed.

An example of the application of this statistical analysis technique utilizes the data of Hand et al. (1965) and two original observations. Figure 7 demonstrates the fit of Equation 1 to four sets of temperature versus swimming speed data for marine dinoflagellates. Table 2 summarizes the equation parameters and their 95% confidence limits and computed maximum swimming speed and its 95% confidence limits. Interestingly, this preliminary analysis suggests that maximum swimming speed increases with cell length (S = 51.08 + 4.09 L, r^2 = 0.94). If generally true, this pattern contradicts previous discussions of the size dependence of swimming speed within bacteria and flagellated or ciliated protozoans (e.g., Holwill 1977). More realistically, a rigorous size dependence of swimming speed is most likely among morphologically similar cells at the genus level or, possibly, along evolutionary lines within a protozoan class like the dinoflagellates (Taylor 1980).

CONCLUSIONS

The data base for the effects of temperature on dinoflagellate swimming speed and orientation from a field perspective can be considerably improved using available technology and developing experimental systems and statistical analyses. This improved data base will allow a more robust characterization of behavioral parameters of biophysical models. Such models can be used to investigate more realistically the interactions between various physical situations in the field and the representative swimming behavior of different dinoflagellate species. This kind of survey will contribute to information on the role that motility plays in allowing dinoflagellates to successfully compete with other algal classes in the sea.

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APPENDIX I

CONFIDENCE LIMITS FOR PREDICTED SWIMMING SPEED AT A GIVEN TEMPERATURE FROM $S = S_A \left(1 - e^{-a(T - T_L)}\right)\left(1 - e^{-b(T_H - T)}\right)$

D. Kamykowski and F.G. Giesbrecht[1]

The SAS User's Guide: Statistics (SAS 1982) describes a nonlinear regression procedure (NLIN). For the present application, the derivative-free (DUD) method of Ralston and Jennrich (1978) is used to perform the least squares fit of Equation A1 to the temperature versus swimming speed data. NLIN provides asymptotic confidence limits for the parameters (a, b, S_A , T_L , T_H) in

$$S = S_A \left(1 - e^{-a(T - T_L)}\right)\left(1 - e^{-b(T_H - T)}\right) \tag{A1}$$

for $T_L \leq T \leq T_H$. Confidence limits for predicted values of swimming speed at a given temperature for this equation, however, require separate calculations. In matrix notation, the variance of a predicted swimming speed at a given temperature is

$$\hat{Var}(\hat{S}) = \left.\frac{\partial S}{\partial \theta}\right|'_{\theta = \hat{\theta}} \hat{V}(\hat{\theta}) \left.\frac{\partial S}{\partial \theta}\right|_{\theta = \hat{\theta}} \tag{A2}$$

where θ is a generalized parameter, $\left.\frac{\partial S}{\partial \theta}\right|_{\theta_0}$ is the vector of partial derivatives of S evaluated at $\theta = \theta_0$, $\left.\frac{\partial S}{\partial \theta}\right|'_{\theta_0}$ is its transpose, and $\hat{V}(\hat{\theta})$ is the estimated variance-covariance matrix of the estimated parameters from NLIN.

The partial derivatives of the parameters are:

$$\frac{\partial S}{\partial a} = S_A (T - T_L) \left(e^{-a(T - T_L)}\right)\left(1 - e^{-b(T_H - T)}\right), \tag{A3}$$

$$\frac{\partial S}{\partial b} = S_A (T_H - T) \left(1 - e^{-a(T - T_L)}\right)\left(e^{-b(T_H - T)}\right), \tag{A4}$$

$$\frac{\partial S}{\partial S_A} = \left(1 - e^{-a(T - T_L)}\right)\left(1 - e^{-b(T_H - T)}\right), \tag{A5}$$

$$\frac{\partial S}{\partial T_L} = -a\ S_A \left(e^{-a(T - T_L)}\right)\left(1 - e^{-b(T_H - T)}\right), \text{ and} \tag{A6}$$

$$\frac{\partial S}{\partial T_H} = b\ S_A \left(1 - e^{-a(T - T_L)}\right)\left(e^{-b(T_H - T)}\right) \tag{A7}$$

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Since $\frac{\partial S}{\partial T} = 0$ cannot be solved precisely, T_M, the temperature at which swimming speed is maximum, is determined by an interactive run advancing at small temperature increments over a temperature range that is known to contain S_M, the maximum swimming speed, by inspection of the best fit curve. T_M is substituted for T in forms of Equations A3−A7 where a, b, S_A, T_L and T_H are provided by NLIN. These equations are then solved to give the vectors

$$\frac{\partial S}{\partial \theta}\Big|_{\theta = \hat{\theta}} \text{ and } \frac{\partial S}{\partial \theta}\Big|_{\theta = \hat{\theta}}.$$

NLIN does not print the variance-covariance matrix, $\hat{V}(\hat{\theta})$, but it does provide the correlation matrix and estimates of the asymptotic standard errors of the five parameters in Equation A1. The variance-covariance matrix can be reconstructed from the estimated correlation matrix and parameter standard errors provided by NLIN. If $\hat{cor}(\hat{\theta}_i, \hat{\theta}_j)$ denotes the correlation between $\hat{\theta}_i$ $\hat{\theta}_j$ and $s(\hat{\theta}_i)$ the standard error of $\hat{\theta}_i$ then the corresponding covariances can be written as

$$\hat{V}(\hat{\theta}_i, \hat{\theta}_j) = \hat{cor}(\hat{\theta}_i, \hat{\theta}_j) \times s(\hat{\theta}_i) \times s(\hat{\theta}_j), \tag{A8}$$

where $\hat{\theta}_i$ and $\hat{\theta}_j$ take on the values a, b, S_A, T_L and T_H.

The vector multiplication takes the form

$$\hat{V}(\hat{S}) = \tag{A9}$$

$$[D(a)\ D(b)\ D(S_A)\ D(T_L)\ D(T_H)]$$

$$\begin{vmatrix} \hat{V}(a,a) & \hat{V}(a,b) & \hat{V}(a,S_A) & \hat{V}(a,T_L) & \hat{V}(a,T_H) \\ \hat{V}(b,a) & \hat{V}(b,b) & \hat{V}(b,S_A) & \hat{V}(b,T_L) & \hat{V}(b,T_H) \\ \hat{V}(S_A,a) & \hat{V}(S_A,b) & \hat{V}(S_A,S_A) & \hat{V}(S_A,T_L) & \hat{V}(S_A,T_H) \\ \hat{V}(T_L,a) & \hat{V}(T_L,b) & \hat{V}(T_L,S_A) & \hat{V}(T_L,T_L) & \hat{V}(T_L,T_H) \\ \hat{V}(T_H,a) & \hat{V}(T_H,b) & \hat{V}(T_H,S_A) & \hat{V}(T_H,T_L) & \hat{V}(T_H,T_H) \end{vmatrix} \begin{vmatrix} D(a) \\ D(b) \\ D(S_A) \\ D(T_L) \\ D(T_H) \end{vmatrix}$$

where the $D(\hat{\theta}_i)$ are the partial derivatives defined by A3−A7 evaluated at the observed parameter estimates, i.e., a, b, S_A, T_L, and T_H. Draper and Smith (1966) is one of several sources of information on the matrix manipulations as applied to statistics and provides a simple account of the solution of A9. The result of these manipulations is the $\hat{VAR}(\hat{S})$ which can be used to compute the confidence limits of S_M at T_M with the appropriate value of "Student's" t.

CHAPTER TWO

MOVEMENTS OF BENTHIC INVERTEBRATES

Migration is as fundamental to, and characteristic of, the life cycles of motile marine invertebrates as it is to fishes or non-aquatic vertebrates and insects. However, the marine milieu challenges merely observing, much less measuring, marine benthic migrations. For this reason, and perhaps because of a generally pervasive vertebrocentrism in zoology, information on benthic migratory orientation, regulation and function is neither well-known nor intensely sought. One even gets the impression sometimes that scientists percieve marine invertebrate migratory performance as either simply explained, irrelevant to migration biology or otherwise uninteresting. Those of us peculiarly motivated to persist in our inquiry of marine invertebrate migrants find these perceptions to be incorrect. We believe that the five papers to follow illustrate migratory phenomena that are more complex, more extraordinary and more approachable to research than recognized heretofore. More so, they may lure some developing migrationist into this fascinating and rewarding area, thereby strengthening our ultimate conceptualization of the mechanisms and adaptiveness of migration.

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EVOLUTION AND MECHANISMS OF MASS SINGLE-FILE MIGRATION IN SPINY LOBSTER: SYNOPSIS[1]

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ABSTRACT

This report summarizes two decades of research on all facets of the migration of the spiny lobster ***Panulirus argus*** (Crustacea: Palinuridae). Autumnal mass migrations in this species involve explosive, localized population movements which are triggered by polar front storms wherein the migrants walk continuously in parallel single-file queues for several days from shallow areas to the edge of oceanic channels. It is hypothesized that mass queuing emerged during past glacial cycles as a mechanism that allowed lobsters to evade the deleterious winter conditions in the food-rich shallows typically exploited by lobsters during warm seasons. Queuing probably evolved from antipredator formations but also serves mass migration by reducing hydrodynamic drag. A proposed neuroendocrine-mediated internal state, or zugunruhe, is probably regulated by seasonal photoperiodic and thermal conditions linked also to molting and reproduction. Recent findings show that sharply increased water motion triggers mass queuing. Complex orientation to hydrodynamic guideposts is suggested to guide migration.

> It is not perhaps too much to expect that the...application of modern techniques, such as underwater frogman observation to the behavior of littoral animals, will produce just those data and ideas necessary to integrate what is yet a rather amorphous mass of information.
>
> (R. Bainbridge 1961)

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INTRODUCTION

Richard Bainbridge's (1961) last sentence in his chapter on migration in the Physiology of Crustacea (Vol. 2) called attention to the fact that while we knew at the time that a wealth of crustaceans migrated, the marine medium had thwarted direct observation and, in turn, deeper insights into the phenomenon. The application of underwater research and other techniques foreseen by him as promising have not yet provided the depth of knowledge comparable to that on insects, birds, or fish but the mass of information is perhaps less amorphous than two decades ago (see reviews by Creutzberg 1975; Herrnkind 1980, 1983; Rebach 1983). The movement patterns of the western Atlantic spiny lobster ***Panulirus argus*** have been the subject of intense study over the last 20 years. Here, I present a synopsis of spiny lobster migration with respect to ecological and evolutionary considerations, long- and short-term climatic features, energetics, physiological regulation, environmental triggering, and orientation. Special emphasis is given to hypotheses of migratory orientation and reporting new findings on the environmental effects triggering the unique mass migrations in single-file "queues" (Fig 1).

MASS MIGRATION: SUMMARY

The various species of Palinuridae occupy marine benthic habitats from the nearshore (< 10 m) to the continental shelf (≈ 40 m) in mainly tropical and subtropical seas but range into the extreme temperate zones (George and Main 1967). Certain tropical species are nonmigratory (e.g., ***Panulirus femorestriga***), while others migrate only in certain areas or ecological conditions (e.g., ***Panulirus guttatus***); many species are characteristically migratory, especially ***Panulirus cygnus*** (western Australia), ***P. argus*** (western Atlantic, Brazil to Bermuda) and ***Jasus edwarsii*** (New Zealand).

Over its range and lifetime, ***P. argus*** exhibits several types of lengthy movements including nomadism during the late juvenile phase and migration by adults in association with vernal reproduction. Mass migrations occur typically in autumn, depending on latitude and climatic factors; October in Bermuda, late October and November in the Bahamas and Florida, December in Yucatan and Belize.

The mass migratory syndrome, summarized below, is based on Herrnkind (1980) and the reports cited therein. Bahamian spiny lobsters during summer and early autumn mainly occupy the extensive shallow (3–10 m) "banks" where food is apparently abundant but shelter is sparse and poor in quality. The nomadic lobsters forage nocturnally on benthic invertebrates, then aggregate by day in exposed clusters about the bases of sea whips and large sponges or, when available, under ledges of rock, seagrass rhizome mats or an occasional coral head. In mid-autumn ever increasing numbers of lobsters emigrate in nocturnal queues from the banks to deeper (10–20 m) rock and coral shelters along the bank fringe. The benign condition of the shallows (moderate temperature of 27–28°C and calm water) is sharply disturbed by the onset of a major polar storm front which typically brings several days of reduced

Figure 1
Migratory queue of spiny lobsters (*Panulirus argus*) in 10-m depth west of Bimini, Bahamas.

temperature (5°C drop in sea temperature), high northerly winds (up to 40 $km \cdot h^{-1}$ sustained) with large sea swells, constant overcast and rain squalls. After such a storm, thousands of lobsters mass migrate throughout the day and night in queues of up to 50 individuals along the bank fringe (Fig 2). Queue bearings are consistent for a given locality but vary markedly over the migratory region (e.g., headings are southerly at Bimini, Bahamas, but northerly near Boca Raton, Florida). Daytime queuing wanes after a few days, leaving the sheltered habitats adjacent to the migratory pathway crowded with lobsters which gradually disperse over several weeks. Tagging studies suggest movement on the order of 30–50 km during the migratory period. Subsequent storm fronts do not stimulate equivalent movements, although mass migrations are reported to follow especially violent winter storms and hurricanes. Dispersal back into the shallows occurs as nomadic nocturnal movements spread over several months; no analogous mass return migration has been documented.

MASS MIGRATION: EVOLUTION

Adaptiveness

Perspective on migratory adaptiveness can be found in Dingle's (1980) excellent comparative discussion, Baker's (1978) migratory compendium, George and Main's (1967) study of the evolution of Palinuridae, and Herrnkind's (1980) discussion of palinurid migration. Determining the selective forces that underlie mass migration requires explanation not merely for the shift in location of migrants but also for its synchrony, specialized locomotory behavior and explosiveness. Some facile migratory functions are improbable, in particular those linked directly to reproduction and spawning. Mating and spawning occur with a strong annual peak in mid- to late spring (April–June in north latitude migrant populations). Gonads are largely inactive in the

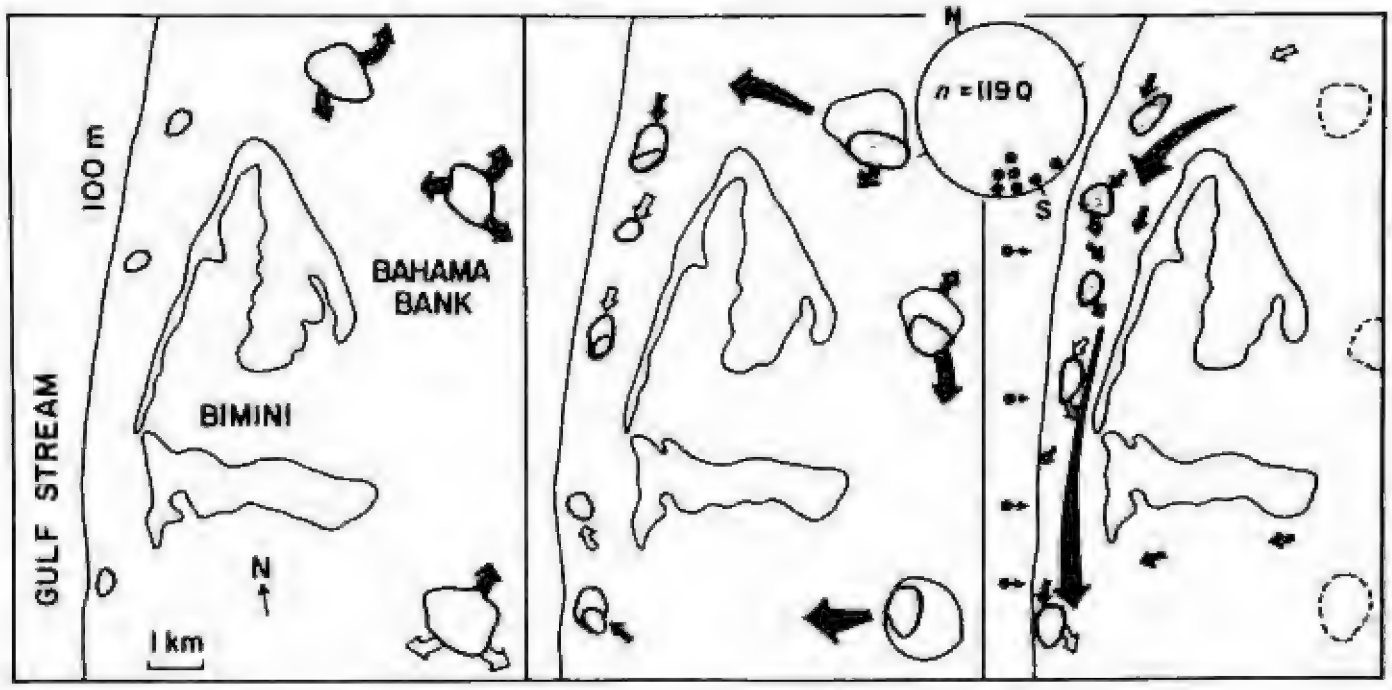

Figure 2

Summary of lobster movements before the mass migratory period (left), during build-up (center), and during diurnal mass queuing near Bimini, Bahamas. Lobsters move nomadically about the shallows east of Bimini until midfall when numbers move westward to the oceanic fringe. Following the first major polar front, thousands of lobsters in queues travel southward along the fringe (right). (Inset) Scattergram of mean bearings of 119 queues recorded at various locations west of Bimini (small dots with arrows).

fall migrants and begin maturing in late winter (Quackenbush 1981). The movement does not serve solely as an ontogenetic habitat shift because migrants in areas such as Yucatan are mostly old adults. Bahamian migrants include both late juveniles and adults, although the bulk comprises individuals in their first year of sexual maturity. Nutritional enhancement also seems unlikely because food abundance undergoes no apparent decline during fall (personal observation). Dispersal by first coalescing then scattering hardly seems consequential to a species rampantly nomadic with one of the most extensive larval broadcasting mechanisms known (Phillips and Sastry 1980).

Evidence favors the hypothesis that migrants evade the physical stresses of probabilistically severe winter cold and water turbulence. The tropical physiology of *P. argus* provides little resistance to severe winter cooling to 10°C as recorded during periodic fish kills in south Florida waters. Substantially reduced locomotory and feeding ability occurs at 12−14°C during severe but seasonally realistic temperature declines. Individuals eventually became moribund and behaviorally unresponsive (Wynne 1978); molters die during exuviation under these conditions (Davis 1978). Our recent work suggests that many migratory lobsters in Florida and Bahamas molt sometime during late fall and early winter (Quackenbush and Herrnkind 1983). Molters in shallow water are most susceptible to direct mortality because thermal conditions there are most extreme (Kanciruk and Herrnkind 1978). The evasion hypothesis is supported by the rapid exodus from the shallows manifested by storm-induced local synchrony, continuous locomotion, energetic advantages of queuing and cessation of intense migration once lobsters reach sheltered habitats on the oceanic fringe.

Paleoclimate and Origin of Mass Migration.

Long-term climatic conditions have had the most profound impact on the evolution of migration in animals and bear directly on any discussion of adaptiveness (see the informative review by Gauthreaux 1980).

The succession of glaciations over the past several 100,000 years caused modulation of two major forcing effects on coastal waters: latitudinally shifting temperature profiles and changing sea levels. For a shallow subtropical lobster like *P. argus*, the temperate limit range is bound by the thermal minima of offshore waters migrants can reach in winter. Vagile species would be expected to exploit warm, food-rich summer shallows, then migrate offshore as conditions deteriorated. Populations of *P. argus* at the present temperate boundary along the northern Gulf of Mexico behave in just this way (W. Herrnkind, unpublished data). During peak glaciation the species range would have been constricted toward low latitudes, while the annual inshore-offshore movements would be adjusted to the redistributed coastal habitats. I contend that the extreme and sharply defined autumnal cooling, during peak glacial periods even in low latitudes, placed a premium on the migratory capability of *P. argus* to allow the species to exploit the shallows yet evade the rigors of winter. The evolution of explosive mass queuing is, perhaps, a product of such conditions. By comparison, *P. guttatus* and *P. laevicauda*, the nonmigratory sympatric congeners of *P. argus*, are limited both in geographic and ecological range. Both latter species occupy mainly coral reef habitats in the Bahamas and Florida and do not occur in the summer shallows of the northern Gulf of Mexico and Carolinas.

In overview, the tropical ancestors of *P. argus* likely exploited the extensive non-reef shallows, characteristic of the tropical western Atlantic, through migratory prowess. Mass migration became specialized through selective action of glacial winters. This efficient migratory behavior that evolved has thereafter permitted the species to sustain its range in temperate regions uninhabitable by its congeners. Moreover, the migratory ability of *P. argus* underlies the numerical prominence of this species by permitting its members access to immense food and habitat resources unattainable by other tropical lobsters of similar physiological constitution.

MASS MIGRATION: MECHANISMS

Energetics

Energetic enhancement characterizes the migratory performance of birds, insects and fishes (Blem 1980). Although lipid storage, increased metabolic efficiency, and behavioral adjustments reducing energetic costs serve those groups, only the latter is presently suspect in spiny lobsters. Moving in queues of 5 or more reduces the average hydrodynamic drag on each lobster by approximately one-half at the migratory walking rate (ca. 1 $km \cdot h^{-1}$, Fig 3, Bill and Herrnkind 1976). The metabolic savings from drag reduction remains to be measured but probably is substantial over a period of five days of walking for 20 hrs per day. Other behavioral features of queuing are

also consistent with drag reduction. Pointing the antennae ahead at maximum queuing speed reduces drag by over 30% as compared to the perpendicular antennal position typical of foraging and other slow movements. Interlobster positioning places each follower within the optimal distance to benefit from the wake trail of its predecessors (Bill 1980). Queuing by numerous individuals is a behavioral specialization for conserving energy during rapid, continuous locomotion over long distances.

Queuing probably evolved from stationary antipredator formations which are exhibited by several species of spiny lobsters, as well as by ***P. argus***, when away from shelter in daylight. Pods, circular "rosettes," and clusters tail-to about sea whips probably provide protection from predaceous fish otherwise capable of attacking the modestly armored abdomen of a solitary lobster. The great shallow banks presently occupied by the bulk of ***P. argus*** populations have little cover, and one often observes barely sheltered pods resting by day. Queuing migrants form into pods by spiraling about the lead animal and reform queues by falling in line behind moving individuals, all the while maintaining tactile contact. Theoretically, this is the most efficient and practical action to both sustain individual proximity and achieve maximum sensory (especially visual) surveillance by a moving group (Treisman 1975).

Priming

The environmental signals that stimulate the neuroendocrine processes directly and prepare animals for migration, and the nature of those processes, are generally reviewed by Meier and Fivizzani (1980). Dorgelo (1976) declared that little is known about such processes in crustaceans and called for active study. Recent reviews of crustacean neuroendocrine processes (e.g., Aiken 1980, Adiyodi and Adiyodi 1970) mention nothing about control of migratory state. Our research since 1977 on seasonal signals and endocrine mechanisms controlling molt and reproduction in spiny lobsters, although very incomplete, provides potential insight.

Premigratory queuing in early fall, and the reduced responsiveness of lobsters to storms outside the fall, suggests some predisposed internal state or zugunruhe analog. Lipcius (in preparation) showed that male pre-reproductive hyperactivity, as well as male and female courtship, were regulated in accord with particular photoperiodic and thermal regimes. Quackenbush (1981) and Quackenbush and Herrnkind (1983) found interactive regulatory effects of photoperiod and temperature on molting physiology which also influence the level of locomotory activity in *P. argus* (Lipcius and Herrnkind 1982). Photoperiodic and thermal features of the fall period, which bring on molting and repress gonadal maturation in *P. argus*, may also organize the neuroendocrine process underlying zugunruhe.

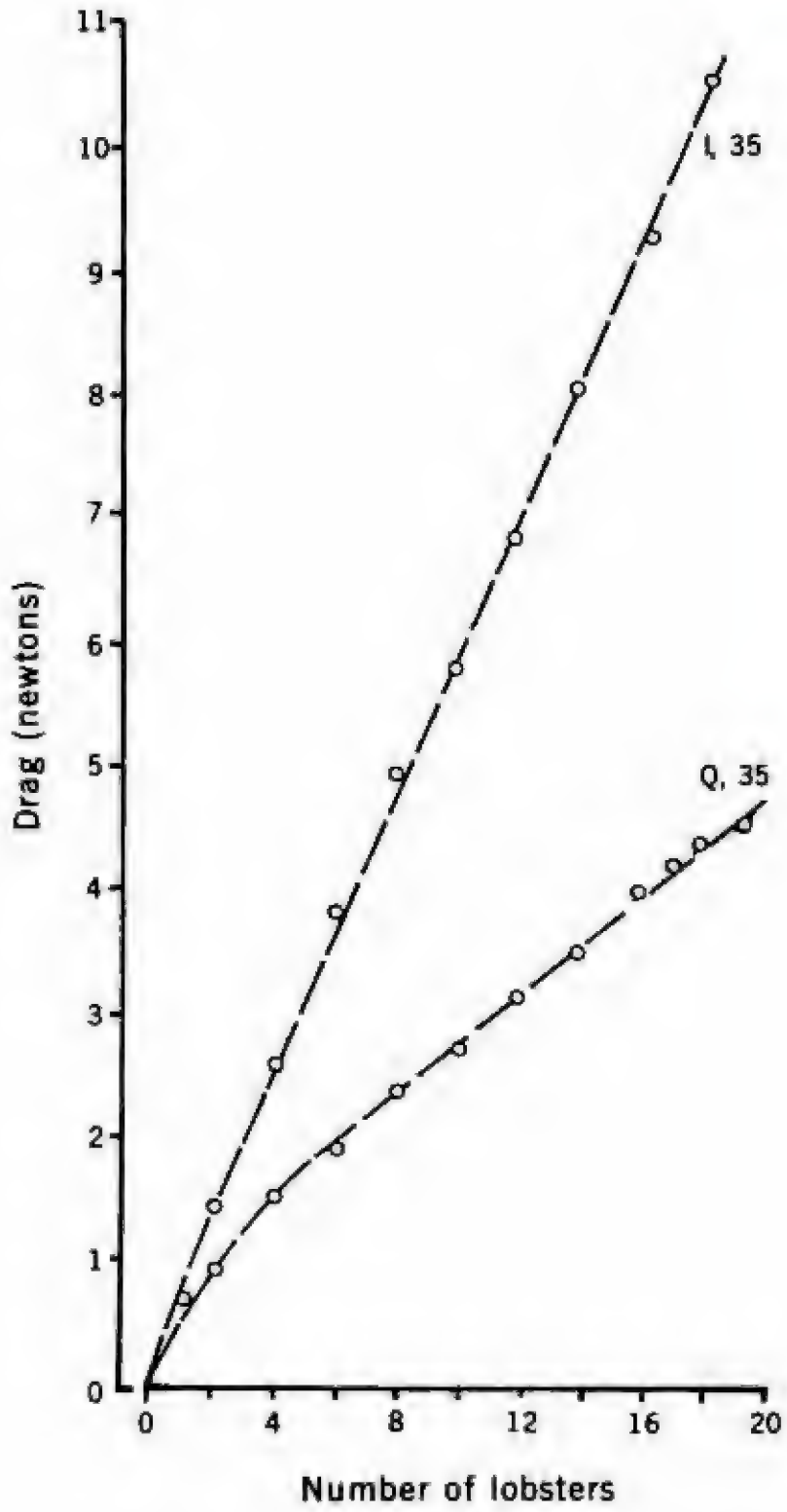

Figure 3

Preserved spiny lobsters towed at migratory speed in queue alignment yield substantially less drag than the summed values for the same lobsters towed individuallly (details in Bill and Herrnkind 1976).

We earlier hypothesized that some storm-related stimulus triggers synchronous mass queuing (Herrnkind and Kanciruk 1978). The sharp temperature drop accompanying storms strongly correlated with queuing activity of lobsters held outdoors in circular pools of free-flowing seawater (Kanciruk and Herrnkind 1978). In addition, because hydrodynamic stimuli strongly influence lobster orientation, the sharply increased water movements accompanying storms such as current flow, wave surge and turbulence, were suspect as well.

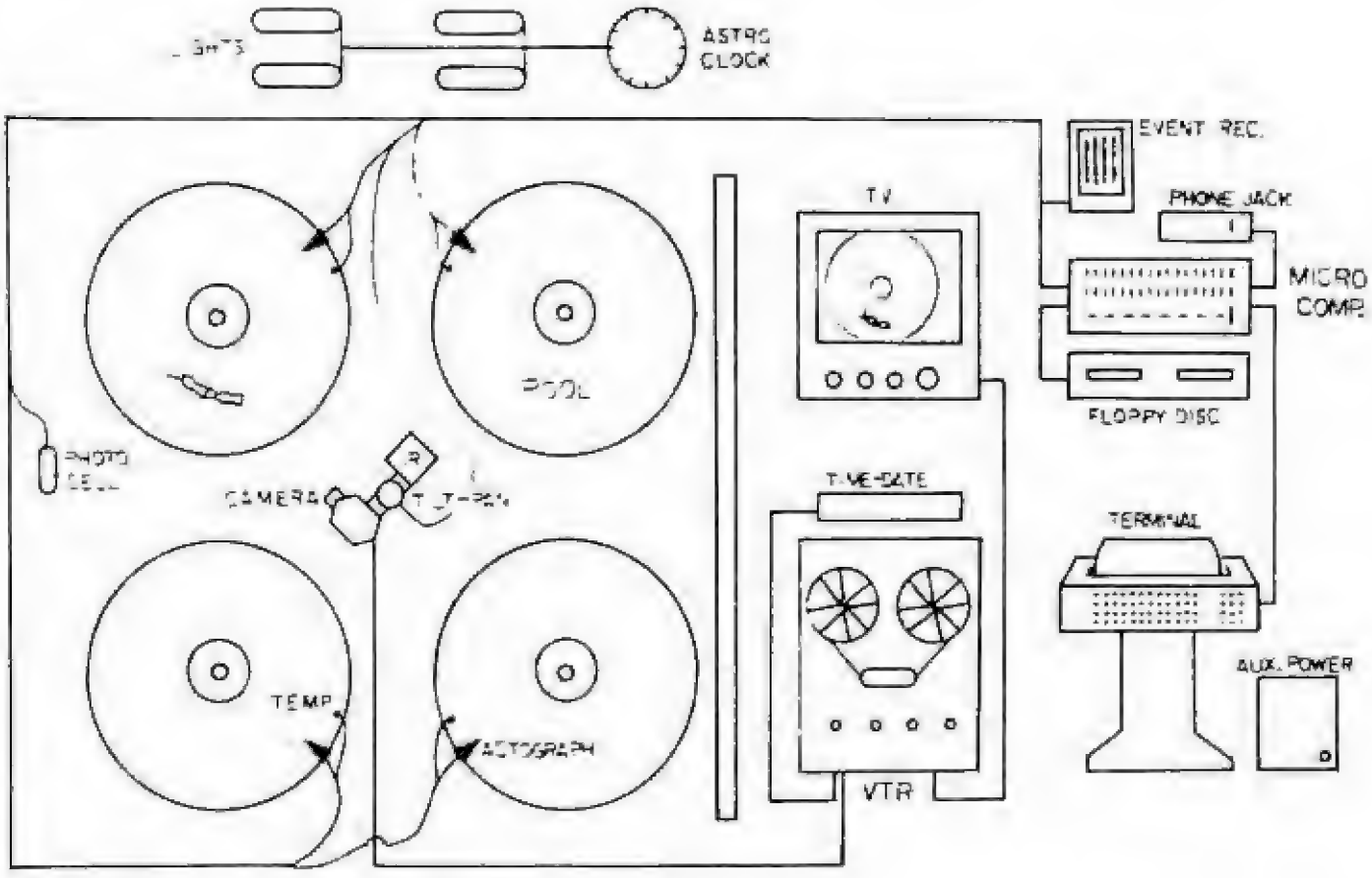

Figure 4

Schematic of the indoor lobster migration pools, environmental controls, and monitoring instruments. Shown are four of six 2000-l pools with independent air-lift seawater recirculation, coarse sand substrate and central concrete den. Temperature is regulated by 1000 W pool heaters; graded sunset and sunrise is controlled by an astronomical clock linked to banks of fluorescent lights. Monitoring instruments include a pan-tilt mounted TV camera with infrared illuminator linked to a time-lapse videotape deck with time-date generator. An additional activity monitor consists of pool-edge actographs constantly recorded on microcomputer floppy discs and on a backup chart-paper event recorder.

Migratory Triggering

Lobsters in circular outdoor pools (2 m dia) queue nearly continuously about the periphery in concert with the passing of autumnal squalls (Kanciruk and Herrnkind 1978). To determine which of the many potential storm-caused stimuli trigger such mini-mass migrations, we tested likely factors in indoor pools with environmental controls and behavioral monitors (Fig 4). Lobsters captured in early fall (before migration) from a known migrant population in the Florida Keys were held under photoperiodic, thermal and salinity levels reigning at the time of capture. The 7–9 lobsters in each pool were fed live crabs (similar to natural diet) and monitored for general activity on a constant recording computer-actograph. The experimental protocol provided natural levels of stimulation on a schedule consistent with field measurements taken during previous migrations. We tested sharply increased current flow (raised from < 1 to 20 $cm \cdot s^{-1}$), reduced temperature (5–6°C decline over 24–36 hrs) and shelter removal, first in combination then individually. The criterion for migratory triggering was defined as the appearance of sustained daytime queuing such as that which occurs in nature only during mass migration. Behavior was monitored continuously by time-lapse videotaping using infrared illumination at night. Up to 4 pools were monitored for 5-min periods each 20 minutes by a panning TV

camera. Treatments lasted for 2–4 days.

The queuing frequency in each test pool that had received stimulation was compared to the queuing frequency in that pool during the last day of ambient conditions prior to a manipulation. Simultaneous controls consisted of adjacent pools retained under ambient conditions. Videotape analysis involved point scan recording of behavioral state (queuing, individual locomotion, inactive).

Two groups of lobsters that had received multiple stimuli emerged from shelter within one hour and formed queues of 3–5 individuals which circled the tank periphery primarily in the downcurrent direction (Fig 5). Thereafter, most individuals remained active for the duration of stimulation, some leaving a queue to briefly feed, change direcion, or rest. This behavior was indistinguishable from that of pool-held lobsters during migration and met all criteria of natural migratory queuing as constrained by pool configuration.

Among individual factors, only the current increase induced mass queuing (3 of 5 groups). Reduced temperature induced a slight increase of daytime queuing in one of five groups but generally suppressed activity in the others (3 groups; Fig 6). Shelter removal yielded slightly increased individual locomotion because lobsters in resting pods along the pool wall were disrupted by foraging individuals, often causing brief periods of walking and resettlement (Fig 6). The groups responding most strongly to current behaved analagously to those stimulated by multiple factors. Again, the queuing direction was predominantly downcurrent (Fig 5).

Behavior of lobsters in the current trials was consistent with a response to water motion rather than locomotion forced by hydrodynamic drag. Lobsters walking upcurrent showed no signs of postural adjustment to severe water motion (i.e., appressing the body to the substrate and anchoring the walking legs). The maximum velocity tested, 20 $cm \cdot s^{-1}$, is only a moderate flow rate in nature; lobsters during field observations readily walked about in velocities of 30 $cm \cdot s^{-1}$. Moreover, water motion was nil in the pool center, providing a rarely-used refuge. Therefore, sharply increased current alone probably serves as a natural trigger to mass queuing although potential stimuli remain untested (e.g., reduced light, turbidity, wave surge).

Several other observations provide potential insights into triggering stimulation, orientation and zugunruhe. Mass queuing was induced once in three trials by use of turbulent water action (no net directional flow) which approximated the water velocity of the current trials (Muller 1981). Behavior differed from the latter only in directionality; lobsters in turbulence queued equally often in either direction about the pool (Fig 5). Increased water motion per se hypothetically triggers migration but some guidepost must provide direction. Although directional choice in the pools was limited to up- or downcurrent, the strong downcurrent response implies that the regional current or wave surge prevalent at the outset of mass movement may set the initial migratory bearing.

Differences in responsiveness of groups and individuals to the identical current stimulus suggests differing internal states affecting susceptibility to migratory queuing. Comparison of pretest queuing frequencies yielded a positive correlation between spontaneous queuing for a group under ambient conditions and the strength of queuing

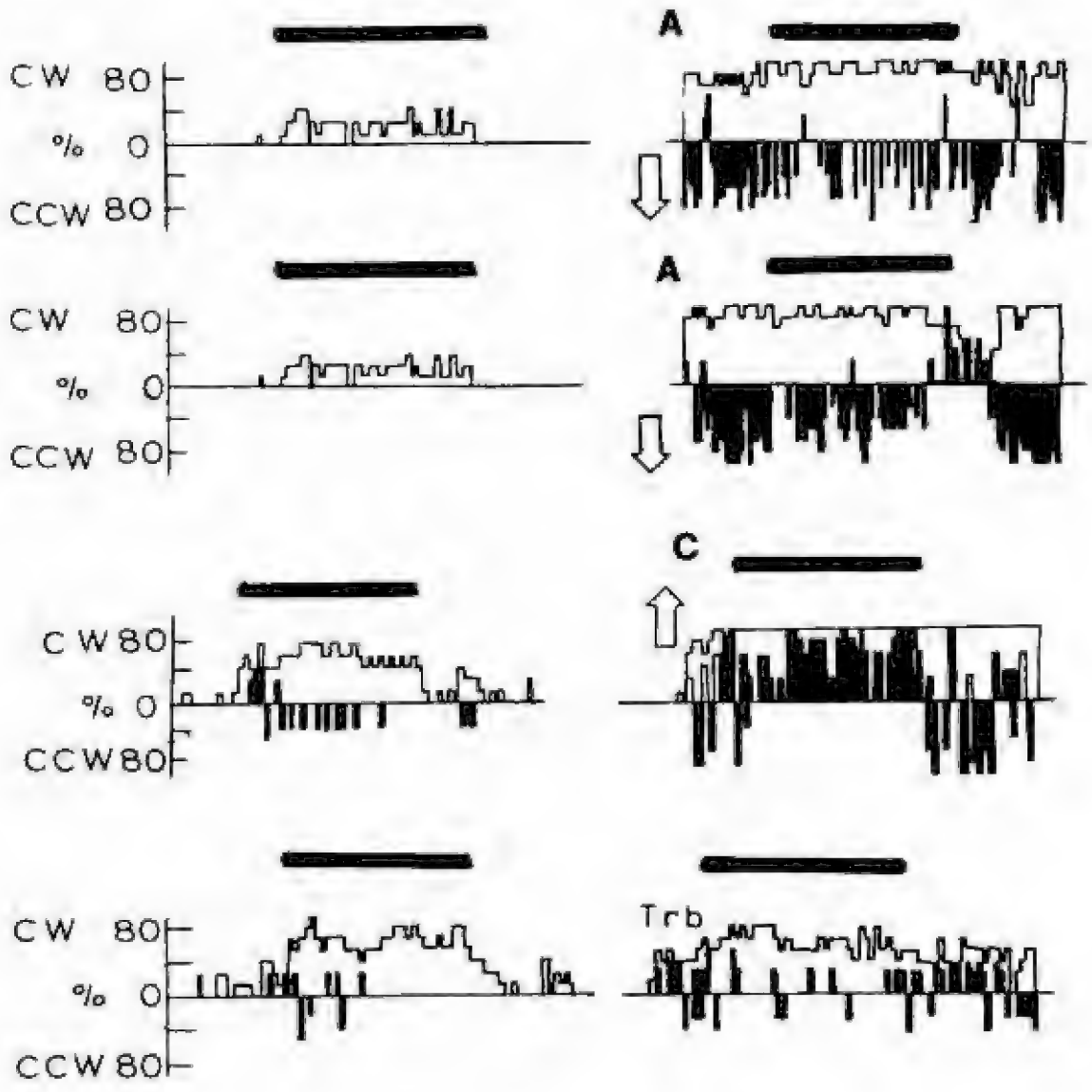

Figure 5

Comparison levels of activity (open histograms) and queuing (darkened histogram) through one day of ambient conditions (left) and one day of stimulation (right). Histogram height shows the percent of lobsters active and queuing, either clockwise (CW) or counterclockwise (CCW). A: stimulation by combinations of current increase, temperature decline and shelter removal. Open arrow denotes current flow direction. C: stimulation by increased current only; ambient temperature and shelter present. Trb: stimulation by turbulent water movement only; ambient temperature and shelter present.

responses of the same group under hydrodynamic stimulation (n = 11; Spearman r = 0.847). I plan to screen lobsters for variation in zugunruhe and further seek understanding of the factors regulating internal states.

Orientation

Spiny lobsters orient accurately both during homing and migration. Although vertebrocentric orientationists typically dismiss nearly everything but bird navigation as "simple," nightly relocating a den from 400 m distance, or maintaining a consistent heading for 10 km through variable topography and hydrodynamic conditions cannot be explained by present orientational knowledge. Excellent reviews of orientational mechanisms appear in Able (1980) for animals generally, Cruetzberg (1975) for marine invertebrates, Rebach (1983) and Herrnkind (1983) for crustaceans, and Herrnkind (1980) for spiny lobsters.

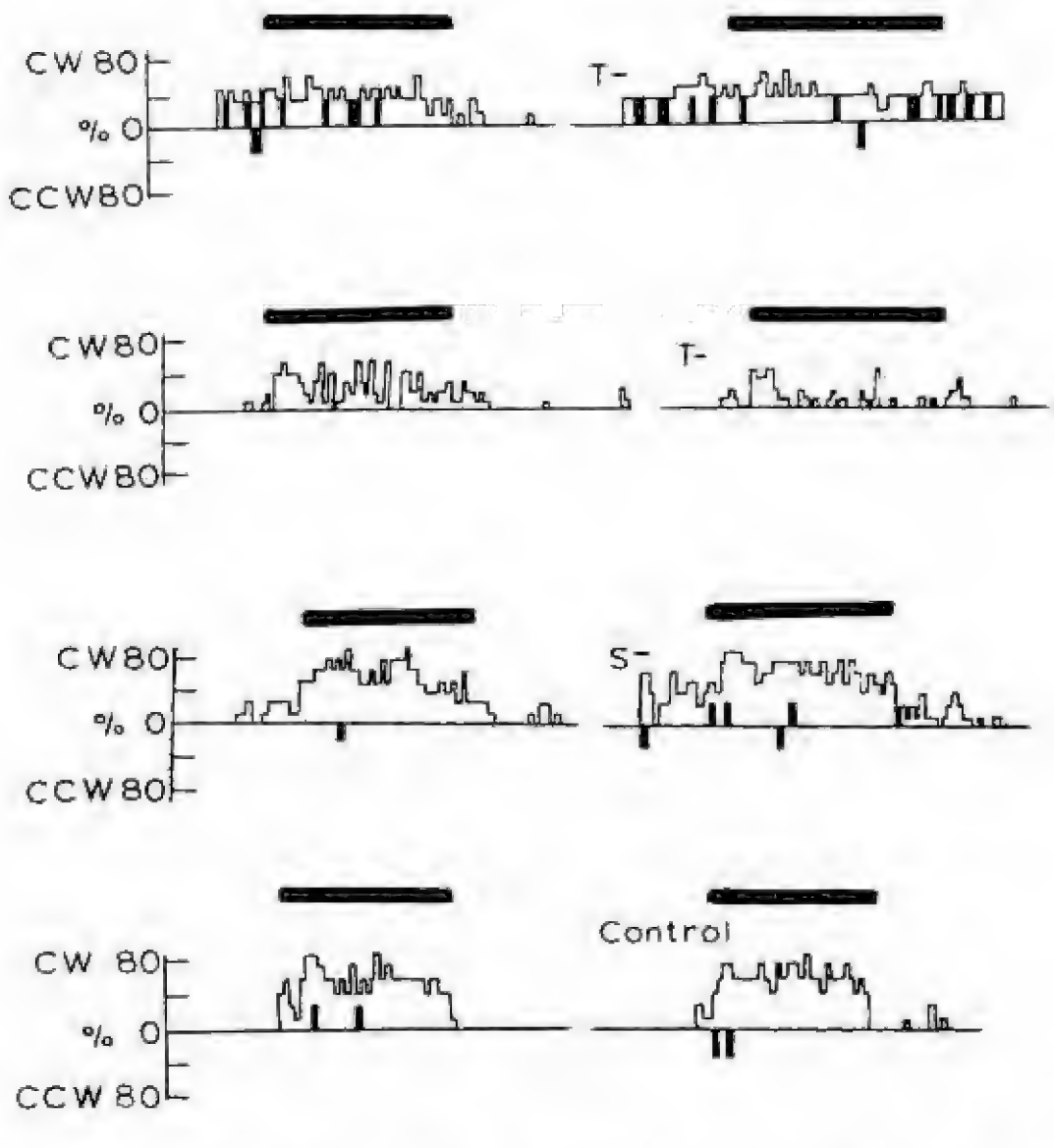

Figure 6

Comparison of activity and queui.gby lobsters receiving sharp temperature declines only (T-), shelter removal only (S-), or left in ambient conditions (Control).

The orientational process underlying migratory guidance must account for establishing and maintaining consistent directionality for 15 km or more. The submarine terrain undulates irregularly in depth from 2 to 20 m with virtually flat sand stretches as well as sharp vertical relief which probably requires detouring. Moreover, optical conditions are typically poor at night and even by day in turbid waters stirred by squalls. Water motion in migratory areas is variable because of changing tidal flow, topographically channeled currents, and wave surge. Certain known crustacean guideposts, including visual orientation to the moon, sun, polarized light or visual landmarks, are unavailable under typical migratory conditions. Simple upslope or downslope response, upwave or downwave surge orientation and bidirectional rheotaxis, whether chemically mediated or not, cannot account for the migratory performance, although those responses can guide lobster orientation under other conditions. Nonmigrant spiny lobsters orient over short distances even when magnets disrupt the earth's magnetic field (Walton and Herrnkind 1977), although magnetic influence on orientation during migration is untested. Guidance by ideothetic or inertial mechanisms seems unlikely to play a primary role. Hydrostatic pressure, thermal or ionic conditions, and waterborne chemicals probably provide cues to location or serve as releasing factors rather than directional guideposts. If known

mechanisms are inadequate, we must hypothesize others.

Our field and wave-tank orientation data suggest menotactic responses to both wave surge and flowing current. Some individual lobsters repeatedly exhibited strong directionality which differed by 90° or more from the current or surge axes during field experiments under nonmigratory conditions (Fig 7). Rayleigh values of 0.9 and higher demonstrate high accuracy by such lobsters despite different bearings among individuals. In fact, individual lobsters released in a waveless lagoon oriented strongly in currents exceeding 5 $cm \cdot s^{-1}$ but showed no common group bearing; individuals released at the same site in still water were disoriented. The hypothesis of menotactic orientation should be tested because its confirmation would open up the possibility that migrants can sustain angular paths relative to hydrodynamic cues or adopt new angles depending on releasing conditions in different parts of the migratory route. For example, as migrants reach oceanic waters, water depth, temperature or chemical cues may cause an orientational shift from upwave to downcurrent.

The behavior of nonmigrants may provide a reasonable assessment of the guidepost array used by spiny lobsters but seemingly does not explain how migrants orient by these guideposts. Just as celestial cues serve the differing orienting needs of local homing and long distance migration in birds, hydrodynamic or other cues may serve lobsters. I hope to artificially induce lobster zugunruhe and thereby compare orientational responses of lobsters before and during migration under controlled conditions.

Strong downcurrent orientation by lobsters triggered to queue in circular pools may imply a significant guiding effect. Migrants, at the outset, conceivably are both triggered by sharply increasing water motion and initially directed by the prevailing current or wave surge. Alternatively, the migratory direction, while not precisely downcurrent, may be oriented to sustain some downcurrent component serving energy conservation. More field data are needed on net current flow and the interaction of wave surge and current vectors in the migratory pathways to evaluate this hypothesis.

Magnetic remanence has been discovered recently in spiny lobster promoting the possibility of magnetic sensitivity used during orientation (Lohmann, in press). The magnetic orientation hypothesis has not been adequately tested in spiny lobsters. With an ultrasonic tracking system and either naturally or artificially induced migratory lobsters, orientation over long distances (exceeding 1 km) could be compared among magnetically disrupted, field-reversed and control specimens.

Of course, some explanation not yet considered may be the correct one; bright ideas accompanied by research data are welcome.

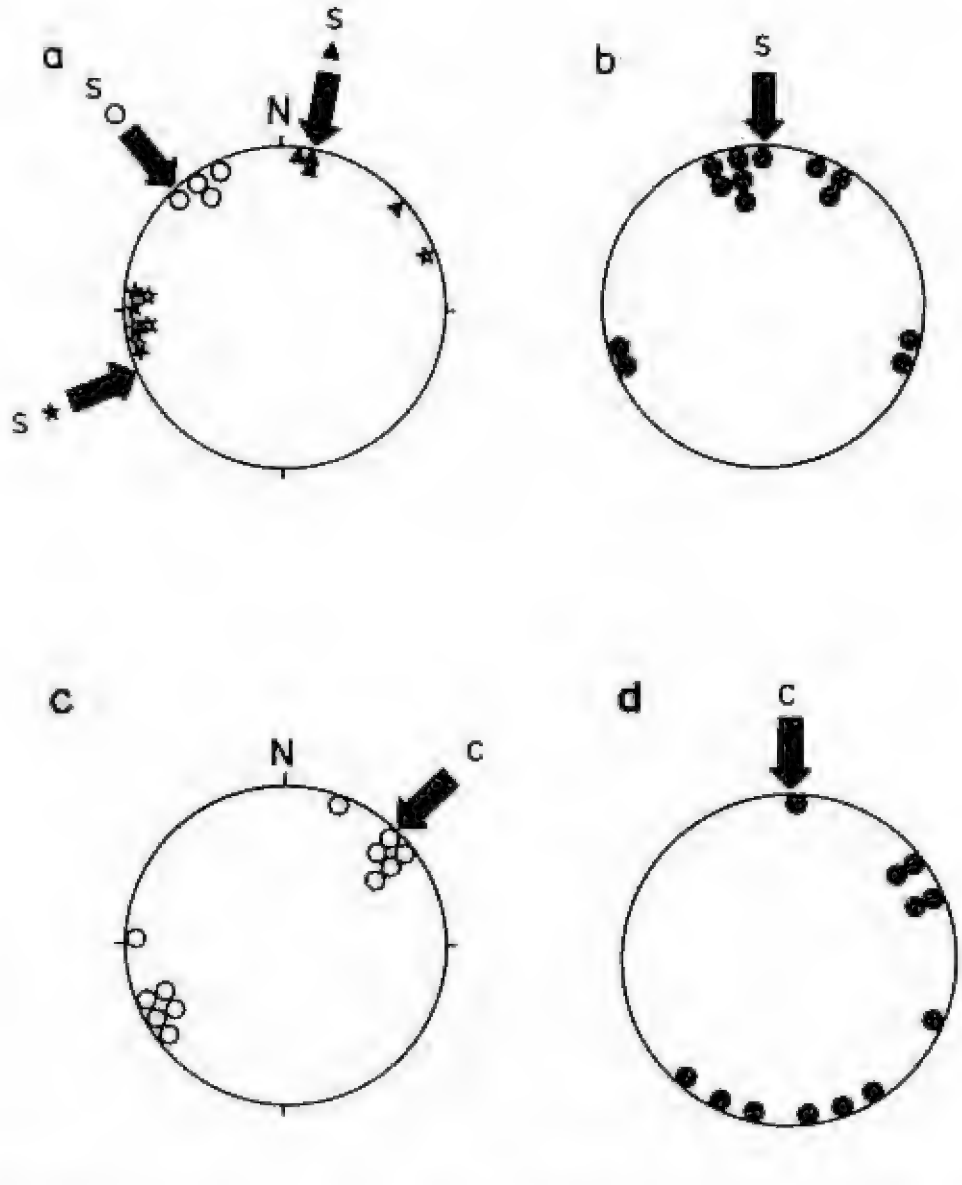

Figure 7

Spiny lobster orientation in field releases. (a) Individuals often orient into the wave surge (i.e., toward the direction of wave approach) on repeated releases. (b) Dots represent statistically significant mean directions based on eight releases of each lobster. The mean directions of well-oriented lobsters cluster in the direction of wave approach although four individuals show markedly different headings. (c) Directions chosen upon six repeated releases of two lobsters in a waveless lagoon with current flow as depicted by the arrow. d. Although the mean bearings of several lobsters show possible positive or negative rheotaxis (into or with the currentsolid arrow), others exhibit directional preferences at various angles from the current axis. Figure based on Herrnkind (1980, 1983).

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MIGRATORY MOLLUSCS, WITH EMPHASIS ON SWIMMING AND ORIENTATION IN THE SEA HARE, *APLYSIA*

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ABSTRACT

Most information about molluscan behavior deals with movement and orientation. Tidal migrations are accomplished by gastropods which inhabit all types of shorelines and by clams on exposed sandy beaches. Up to 90 m of horizontal movement may occur during one tidal cycle. Movement may be active, and guided by phototaxis, geotaxis, or orientation to waves, or it may be passive and involve controlled displacement by wave action. Annual and reproductive migrations are described for intertidal and subtidal gastropods, and octopods. Similar migrations claimed for nudibranchs and scallops are questionable.

The sea hare ***Aplysia brasiliana*** is capable of long-distance migration. Sea hares can swim continuously at the surface for more than 2 h, and can cover distances exceeding 1 km. They apparently can detect wave surge with the rhinophores, can use celestial cues in orientation, and may be able to see objects above the water's surface. In southwest Florida, the abundance of benthic macroalgae, the food of sea hares, peaks in shallow water grassbeds in midwinter and declines drastically by summer. Furthermore, late summer temperatures in shallow water approach or exceed the lethal limit for ***A. brasiliana***. In response to these factors, adult sea hares probably migrate (by swimming) from deep to shallow water in the spring and juveniles, from shallow to deep water in midsummer. Further tagging and tracking studies are needed to clarify basic questions about migration in ***Aplysia*** and other molluscs.

INTRODUCTION

The Mollusca comprise the second largest phylum of animals, and its modern representatives exhibit a great diversity of structural designs and life history strategies. Despite their status, however, much less is known about the behavior of molluscs than of many other groups. The reasons for this situation are that, prior to the last few decades, the primary emphasis of molluscan research was on the shell rather than on the animal which built it and that ethology has traditionally emphasized relatively fast-moving animals such as vertebrates and insects.

Most existing data on molluscan behavior concern locomotion and orientation, primarily of easily accessible intertidal species. Homing in limpets and chitons has been studied for over a century. Other research has explored how gastropods maintain their intertidal position and has involved experiments on phototaxis and geotaxis, and tracking snails displaced short distances in the field. Tidal and seasonal migrations have been documented directly or inferred from life history data for numerous species.

The movement patterns of molluscs have not been reviewed previously, and a thorough review is needed. However, due to space limitations here, I omit discussion of migrations in pelagic cephalopods and planktonic molluscs, of homing in gastropods, chitons, and octopods, and of some of the simple daily movements of gastropods and bivalves. I review the migratory movements of benthic molluscs, and I summarize research on the apparent migratory movements and orientational strategies in the sea hare ***Aplysia brasiliana***. I do not provide an exhaustive bibliography, but I do cite articles through which the interested reader can access the literature.

MIGRATIONS BY MOLLUSCS

Tidal Migrations

Highly mobile marine animals such as fishes and crabs regularly move in and out of the intertidal zone with the tide in order to exploit its periodically available resources. While some intertidal molluscs are sessile, many others are motile; and despite their more modest locomotory abilities, many motile molluscs also exhibit distinct movement patterns synchronous with the tides.

Protected Shores—Low wave energy beaches often have a mixed sand-mud bottom and a gradual slope. These conditions permit establishment of vegetation in many locations and colonization of vegetation and the bottom by motile molluscs. Thus, tidal migrations may be directed either vertically or horizontally in this habitat.

Along northern Gulf of Mexico beaches, marsh periwinkles (***Littorina irrorata***) scrape organic material from the substratum at low tide, then ascend plant stems at high tide. Plant stems are located visually. The cyclic movement minimizes their exposure to predators active in the intertidal zone at high tide, such as crown conchs (***Melongena corona***), blue crabs and fishes (Hamilton 1977). A similar vertical migration on plants is made by the snails ***Melampus bidentatus*** and ***Cerithidea scalariformis*** in Gulf marshes, and on African mangroves by *C. **decollata*** (Cockcroft and Forbes 1981; see also Kitting, this volume).

Melongena undergo a horizontal tidal migration on some protected beaches along the northern Gulf of Mexico. After being covered by the ascending tide, conchs move out of the substratum and crawl up to 30 m shoreward, where they search for infaunal clams and *L. **irrorata*** on short plant stems. Later they move back offshore, and soon after being stranded by the descending tide they bury in the substratum again (Fig 1). A similar onshore-offshore movement is reported for the detritivore ***Bursatella leachii*** (Henry 1952), but the ecological advantage of their behavior is less

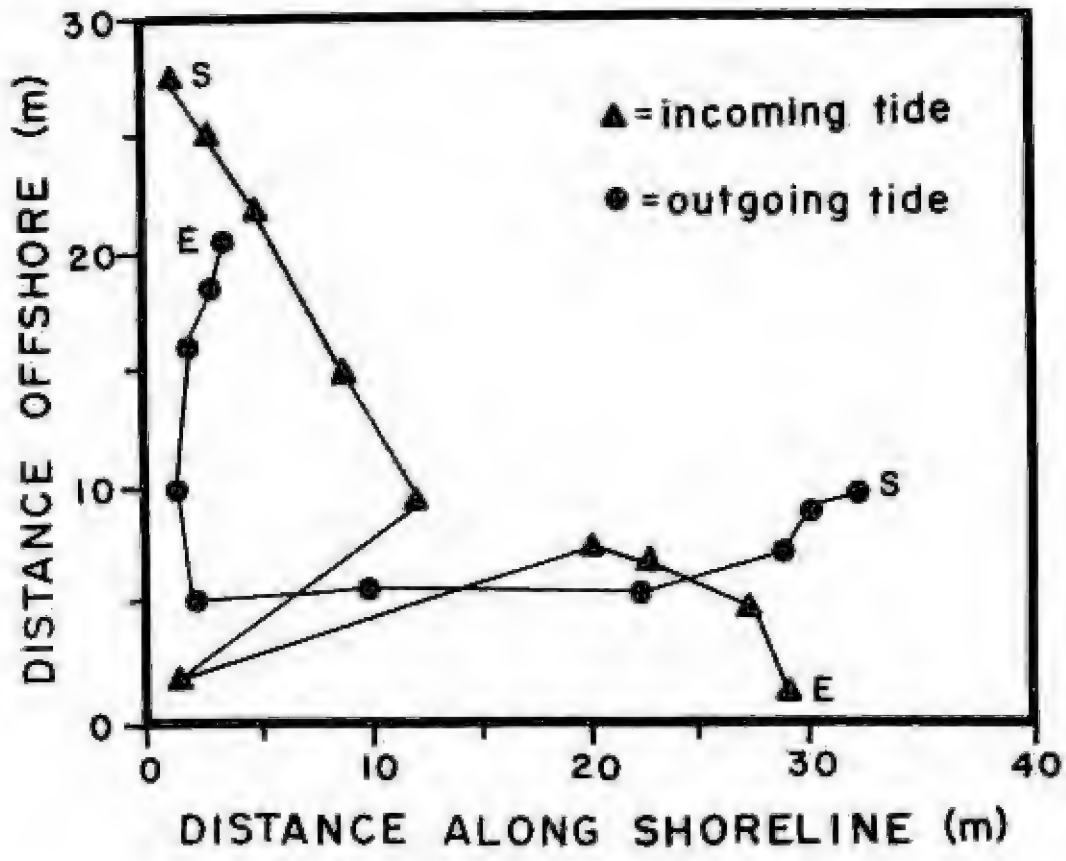

Figure 1
Sequential positions of two *Melongena corona* on a protected beach in northwest Florida during different tidal phases (S = start; E = end).

clear. The orientational guideposts used by these molluscs have not been identified, but wave involvement seems likely. Other gastropods are known to detect waves (Gendron 1977, Hamilton and Russell 1982a).

Exposed Sandy Shores—Most molluscs inhabiting exposed sandy beaches live beneath the sand, yet several groups undergo substantial horizontal migrations with the tides. On the ascending tide the coquina clam (*Donax*) ejects from the sand just as a wave breaks; it is transported up the beach, where it quickly reburies before the swash drains. On the descending tide, the clam ejects into the seaward-flowing swash; it is transported down the beach, where it reburies before the next wave breaks. For some *Donax* species this tidal migration does not occur in all populations (Mikkelsen 1981) and at all times of year (Leber 1982).

Bullia, a carnivorous prosobranch, may move a total of 90 m horizontally over one tidal cycle on South African and Indian beaches. Displacement is controlled by a timely combination of ejection and burying, as in *Donax*, and the foot may be extended as a "sail" during displacement (McLachlan, Wooldridge and Van der Horst 1979). Similar migrations may occur in *Olivella* and *Terebra*.

The adaptive function of these migrations may be to maintain an optimal intertidal position for feeding or to minimize exposure to predators. The use of water flow to facilitate horizontal movement by these molluscs is analogous to the use of tidal currents for displacement by various marine animals which alternate periods of swimming with periods of rest on the bottom.

Exposed Rocky Shores—Distinct tidal migrations seem rare among molluscs that inhabit exposed rocky intertidal zones. The tidal migration of *Nerita textilis* on an almost vertical rock cliff in Somalia (Vannini and Chelazzi 1978) is one clearly

documented example. Several researchers conclude, on the basis of records of day-to-day positions, that other rocky shore gastropods move randomly (Underwood 1977, Petraitis 1982). Tidal movement patterns could easily be missed by this observational method. Horizontal tidal migrations in rocky intertidal zones may be unnecessary because of the abundance of refugia (tide pools, crevices), or may be incompatible with the high species diversity and vertical zonation often characteristic of this habitat.

Annual and Reproductive Migrations

The physicochemical features of surface waters change considerably with season at all but tropical latitudes, and many marine animals undergo annual migrations coincident with these changes. In molluscs that live for several years, a complete migration cycle may occur several times during the lifetime of one animal; only the later cycles coincide with reproductive behavior. In species with one-year or shorter life cycles, different life history stages are usually involved in one migration cycle.

Intertidal Migrants—Fall offshore and spring onshore migrations have been reported at temperate and boreal latitudes for *Nassarius* (Borowsky 1979, Tallmark 1980), *Thais* (Moulton 1962), *Urosalpinx* (Carriker 1954), several littorinids (Batchelder 1915, Williams and Ellis 1975), the Antarctic limpet *Patinigera* (Branch 1975), *Donax parvula* (Leber 1982), and freshwater gastropods (Clampitt 1974). These migrations reduce exposure to cold stress during winter. Late spring offshore and early fall onshore migrations are reported for the limpets *Patella* and *Acmaea* (Branch 1975), and may reduce heat stress during the summer. *Strombus tricornis*, *Cypraea*, and *Turbo* reportedly migrate toward cooler offshore waters during the summer on a Saudi Arabian reef flat (Hughes 1977). Whether migrations occur at all locations within a species' range may depend on intertidal slope and climatic conditions.

Annual migrations are linked to reproduction in some gastropods. Adult *Littorina brevicula* probably spawn during the late winter, while positioned near the low tide line, before commencing their spring onshore migration (Kojima 1959). Juvenile *Patella* (Branch 1975), *Cellana* (Corpuz 1980), and *L. littorea* (Smith and Newell 1955) settle out below the low tide line and gradually migrate onshore as they grow; other intertidal species probably undergo similar migrations, which undoubtedly reflect size-dependent acquisition of resistance to intertidal stresses. *Gibbula* and *Monodonta* migrate upshore to spawn in the spring and early summer (Underwood 1973). The orientational mechanisms involved in the annual migrations of most intertidal gastropods probably involve simple phototaxis and geotaxis.

Subtidal Migrants—Hesse's (1979) study of *Strombus gigas* is one of the best documented examples of annual migration in any mollusc. She tagged 213 conchs and conducted 85 relocation searches over 1 year. Distinct migrations were directed offshore in September and onshore in March, with conchs traveling an average (straight-line) speed of 98 $m \cdot day^{-1}$ while migrating. The migration may be related to avoidance of high wave surge near the shore in winter, and not to avoidance of cold water temperatures.

A massive shoreward migration in January is reported for juvenile ***Bursatella*** in Florida, with queues of animals orienting perpendicular to wave fronts (Lowe and Turner 1976). Benthic *Octopus* reportedly migrate offshore in the fall and onshore in the spring in the English Channel, especially during abnormally cold winters (Rees and Lumby 1954).

It is commonly reported that adult opisthobranch gastropods appear suddenly in shallow water where they mate, lay eggs and die. Adult appearance in shallow water is speculated to result from either a mass migration of adults or a gradual migration (with growth) of juveniles that originally settled offshore. On the basis of long-term sampling studies of intertidal populations, Miller (1962) and Nybakken (1978) rejected the claim that nudibranchs migrate. Nybakken suggests that the "sudden appearances" of nudibranchs may actually reflect the sudden adoption of less cryptic habits by sexually active adults.

Reports by fishermen of sudden appearances or disappearances of scallop "beds" have led to the claim that scallops migrate. A scallop may swim for a few minutes when escaping a benthic predator, or on other occasions, and local movements may be facilitated by currents (Gruffydd 1976). However, direct observations and tagging data reveal no tendency for long distance or seasonal movements (Baird 1954, Hartnoll 1967).

SWIMMING IN SEA HARES AND THE QUESTION OF MIGRATION

The sea hare ***Aplysia*** is a popular model for neuroethological research. Over 1,300 publications on ***Aplysia*** in just the last decade provide abundant anatomical, physiological and laboratory-behavioral information. However, much less is known of the natural behavior and ecology of this opisthobranch gastropod.

Studies of ***Aplysia brasiliana*** along the west coast of Florida reveal an annual sequence of life history events. In late winter and early spring, large numbers of adults are seen swimming near the surface in bays and are found in shallow water seagrass beds feeding on macroalgae, copulating and laying eggs. The average size of animals found stranded on beaches decreases steadily into the late spring, apparently as a combined result of adult mortality and recruitment of newly-settled juveniles. By midsummer, sea hares are rarely found either swimming or stranded on beaches (Hamilton, Russell and Ambrose 1982). A similar seasonal pattern of abundance is reported for *A. **brasiliana*** on the Brazilian coast by Sawaya and Leahy (1971).

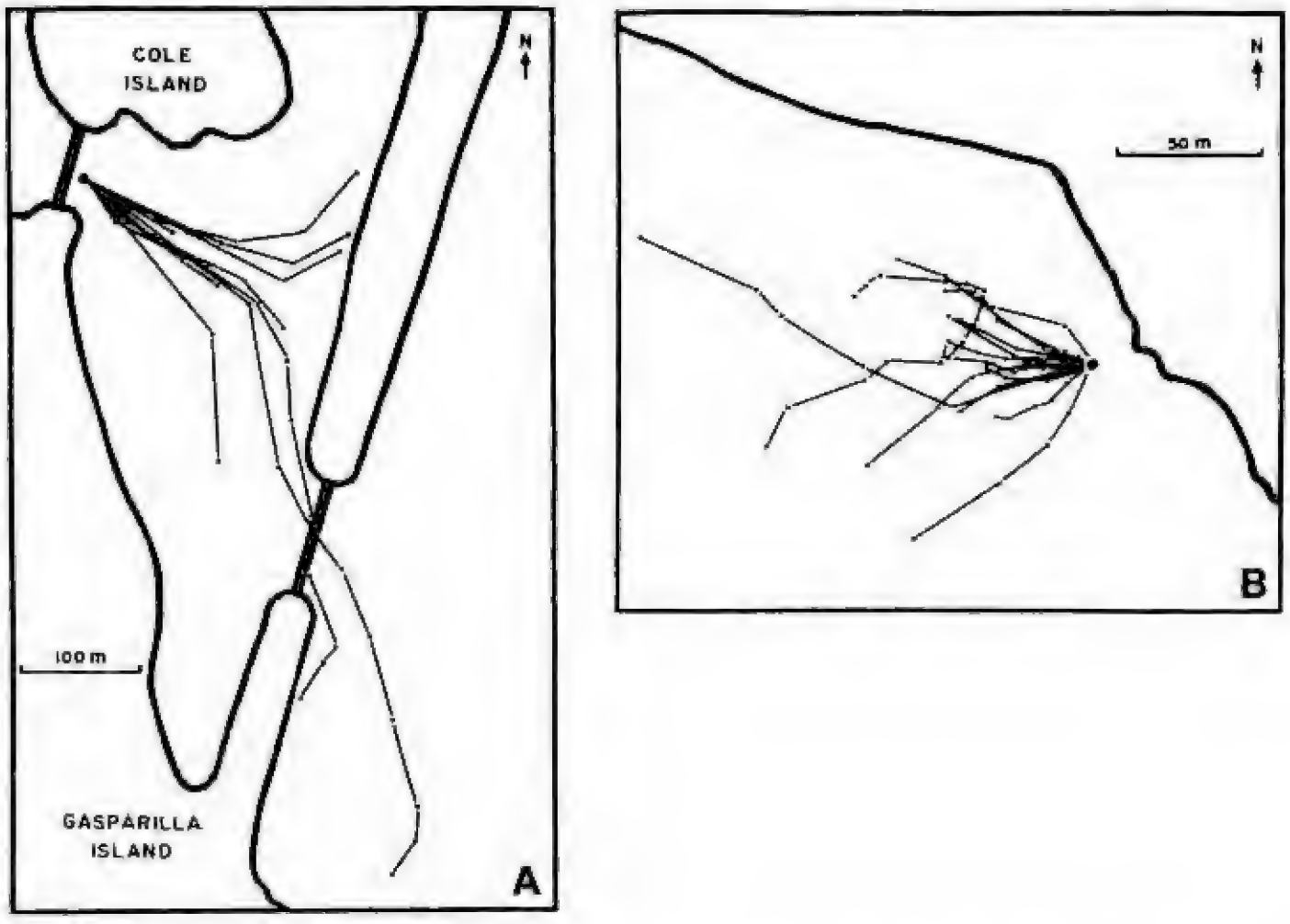

Figure 2

Tracks of surface-swimming sea hares. Tracks are based on positions at 3-min intervals. One group (A) was released in B3 Lagoon during a strong incoming tidal current, and the other group (B) was released at Mote Beach when current speeds were much slower (After Hamilton, in press).

Migration of adult *Aplysia* from deep to shallow water in late winter, followed by migration of juveniles from shallow to deep water during the summer, could account for the changes in sea hare size and abundance observed in the shallow water of bays during the spring. If such a migration occurs, then there ought to be an ecologically sensible reason for undertaking the migration and an adequate means of traveling the required distances. Along the southwest coast of Florida, there appears to be both a reason and a means for *A. brasiliana* to migrate. Our research has concentrated on swimming and its orientation, so I summarize those data before discussing possible reasons for a migration.

Swimming Capabilities

Although sea hares are primarily benthic, they often swim just beneath the water surface in protected bays and tidal inlets (Hamilton and Ambrose 1975). Swimming is accomplished by the rhythmic closure over the dorsum of two large lateral flaps, the parapodia. Water speeds from 2.5 to 14 $m \cdot min^{-1}$ are achieved. Tracks of swimming animals show that the behavior is an effective means of horizontal movement (Fig 2). The farthest swimming animal that I tracked (not shown) traveled 953 m in 114 min and was assisted by a weak current during part of its swim. A strong tidal current can result in even faster ground speeds; several of the animals released in B3 Lagoon on a

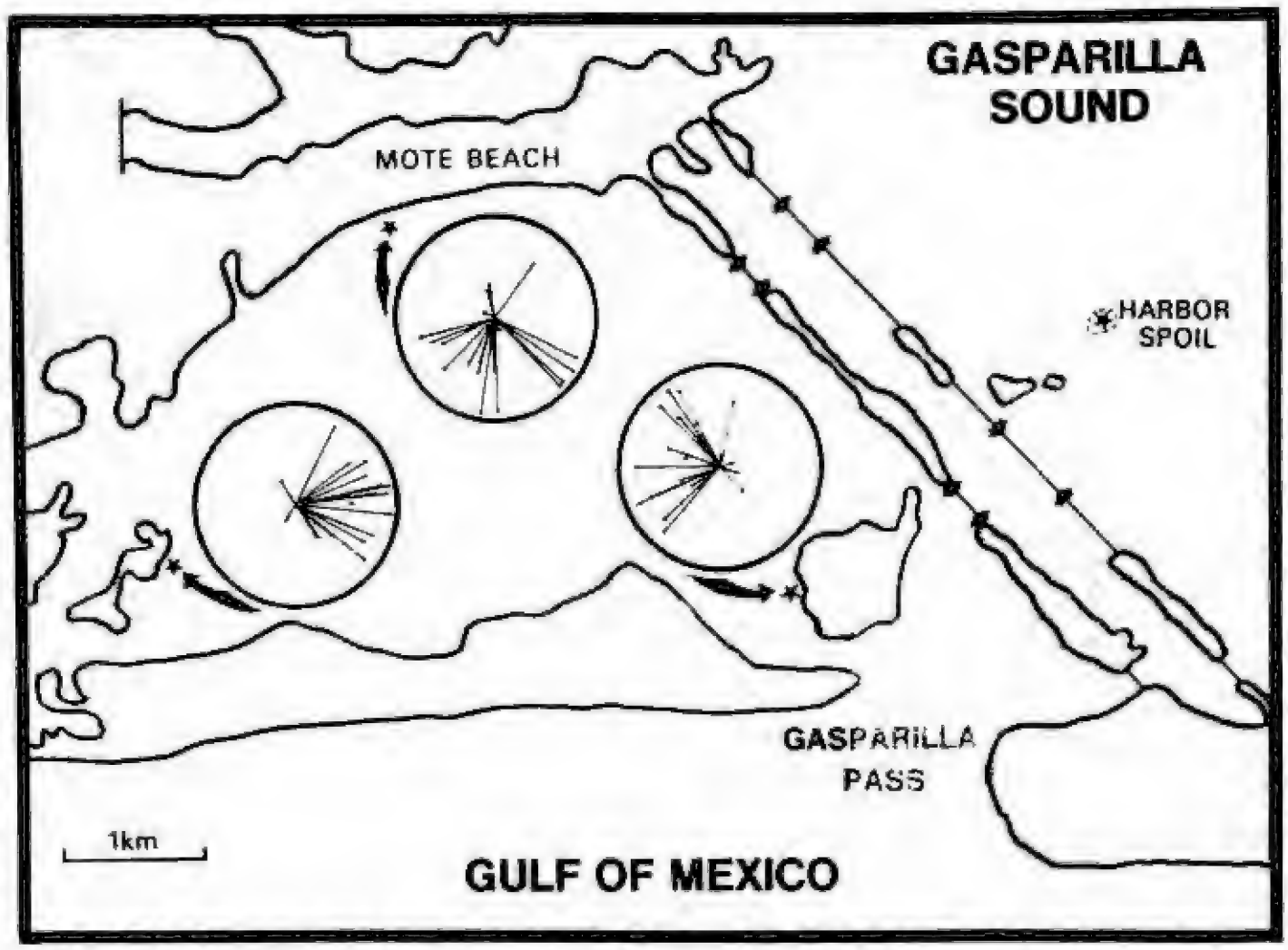

Figure 3

Map of the Placida Harbor, Florida study area showing distributions of mean vectors for the swimming headings (↑ = directions of thrust vectors) by groups of 20 sea hares released near three shorelines which have different offshore directions. Each mean vector is based on five releases per animal (After Hamilton and Russell 1982a).

strong incoming tide (Fig 2A) traveled at speeds exceeding 40 $m \cdot min^{-1}$.

Early in this research we sought a repeatable swimming response which could subsequently be examined under different experimental conditions in order to identify some of the orientational guideposts and sensory modalities involved in swimming. Selection would favor an offshore-oriented swimming response by sea hares finding themselves in shallow near-shore waters because their vestigial shell provides no protection from desiccation stress if they become stranded out of water. We found that *Aplysia* released near shorelines in water 15 to 65 cm deep showed a significant tendency to swim offshore, regardless of the shoreline direction (Fig 3).

In order to identify the orientational guideposts used to determine the offshore direction, 370 releases of 74 animals were conducted at the same location at Mote Beach (see Fig 3). Bottom slope was less than 2° and trees to 10 m tall grew supratidally. Analysis of the distributions of directions taken by the sea hares, relative to the direction of each potential guidepost variable when each animal was tested, indicated that the primary guidepost was wave direction. The ability of swimming sea hares to orient into the waves was confirmed by an additional series of releases which were conducted at a shallow-water dredge spoil located about 475 m from any shore

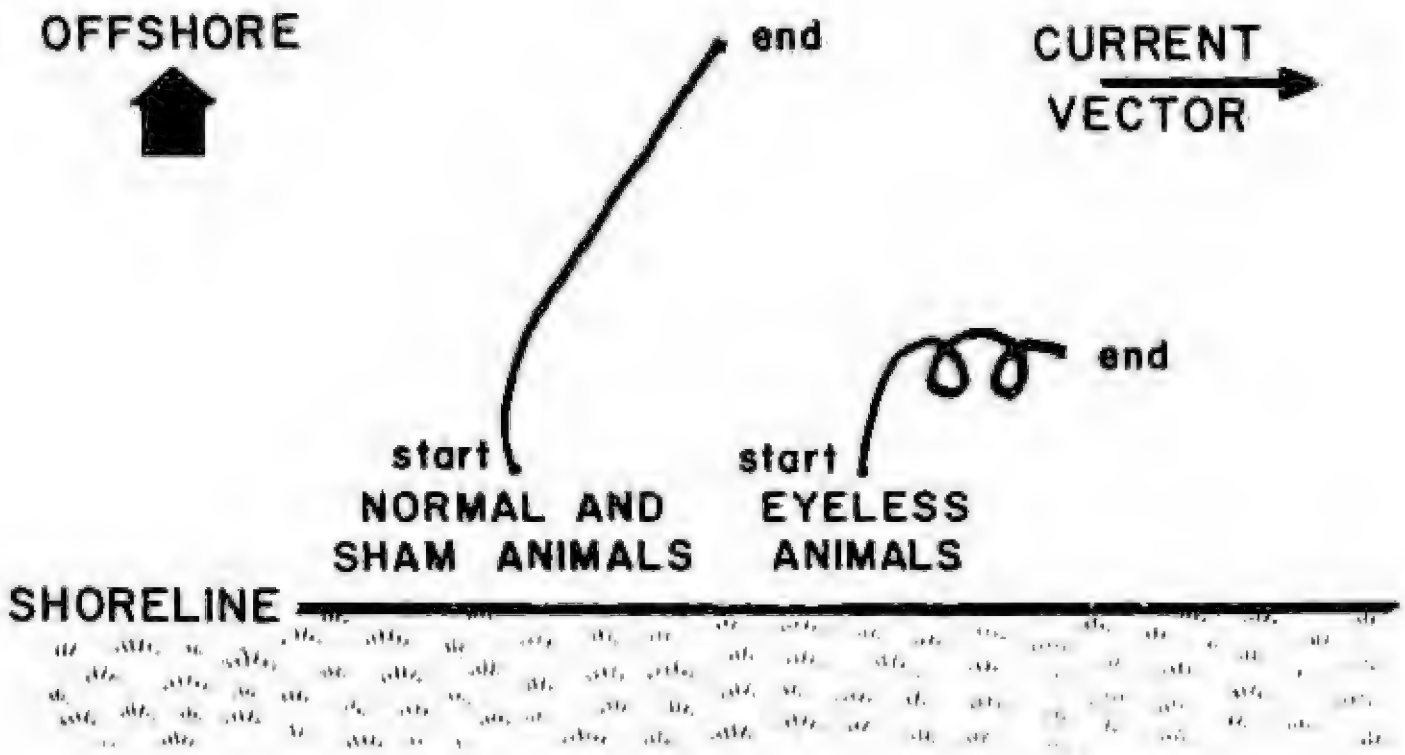

Figure 4

Diagramatic summary of oriented responses of normal, sham, and eyeless sea hares released near a shoreline (Based on Hamilton and Russell 1982a).

(see "Harbor Spoil" in Fig 3). Wind and wave direction changed over the period of these releases, yet the sea hares swam into the waves regardless of their direction. Wave direction seemed a logical guidepost for this response because waves moving onshore refract such that their direction of travel becomes increasingly perpendicular to the shoreline.

Because waves are sometimes absent and because some other animals depend on a hierarchy of guideposts for orientation, we also examined the offshore-oriented response of sea hares when waves were negligible. Sixty releases of 12 animals were conducted at Mote Beach when wave heights were 0 to 2 cm. The 2-cm waves were too small to be refracted at the depth of the release site, and were traveling parallel to the shoreline, instead of perpendicular to it. The 12 sea hares still swam in the offshore direction, suggesting that a second guidepost was involved under these conditions. The second guidepost has not been identified, but swimming sea hares can visually orient to celestial cues (see below) and probably can see some objects above the water surface (Hamilton, in press).

To identify the sensory modalities used in offshore-oriented swimming, two sets of releases were conducted at Mote Beach using animals with ablated sense organs. In one set, 270 releases were conducted with 54 animals. One-third were normal, one-third had their eyes ablated by cauterization, and one-third were sham cauterized. The normal and sham-cauterized animals oriented straight offshore. The eyeless animals started swimming straight offshore, but after only 3 to 4 m of travel, they

began following circular paths and were carried parallel to the beach by the alongshore current (Fig 4). In the second set, 300 releases were conducted with 60 animals. One-third were normal, one-third had their oral tentacles removed, and one-third had their rhinophores removed. The normal and oral tentacleless animals oriented straight offshore; the rhinophoreless animals followed straight paths throughout their swims, but they oriented randomly as a group.

The ablation experiments suggested that two sensory modalities are involved in offshore-oriented swimming. The random orientation of animals that lacked rhinophores suggested that the guidepost cue for offshore direction (presumably waves) is detected by the rhinophores. The failure of eyeless animals to follow a consistent offshore heading suggested that vision might be involved in maintaining a straight path once a sea hare is swimming near the surface (Hamilton and Russell 1982a).

The role of vision in the orientation of swimming was explored further by returning to the Harbor Spoil site and testing sea hares in cone-shaped arenas which were mounted on posts. The arenas were filled with enough water for the animals to swim, but not enough for them to be able to see any shoreline objects. Each test animal was allowed to swim across the adjacent sand flat for 45 sec before being picked up and placed at the bottom of an arena. It usually recommenced swimming immediately, and we observed its heading every 30 sec for 3 min through the clear bottom of the arena. Sea hares with no cover over the arena ($n = 17$) or with a clear plastic cover ($n = 20$) showed a significant tendency to swim in the same direction in the arena as they had been going at the end of their 45-sec free-swimming experience on the sand flat. However, when light from above was diffused by a white plastic cover, sea hares ($n = 20$) oriented randomly. These results suggested that a clear view of the sky is involved in maintaining a swimming direction (Hamilton and Russell 1982b).

One final aspect of sea hare swimming behavior is especially intriguing. When the current speed is higher than average, sea hares modulate their swimming thrust relative to the angular difference between their heading and the current direction (the current aspect); their water speeds are greatest when swimming into the current, least when swimming with the current, and intermediate when swimming across current. A similar Thrust Modulation Response (TMR) is also seen in migratory birds (Bloch and Bruderer 1982). There is considerable variability in the TMR of both sea hares and birds (Hamilton 1984).

The method of determining the direction in which the surrounding medium (water or air) is moving and the adaptive function of the TMR are both unknown. Sea hares and birds deprived of normal visual information still show the TMR (Hamilton and Russell 1982a; Able, Bingman, Kerlinger and Gergits 1982), a finding which indicates the involvement of some method of detecting the moving medium's direction without reference to fixed landmarks. For all swimming or flying animals there should be a single water speed or air speed that maximizes the distance traveled per unit of energy expended; all other speeds would be sub-optimal. (This water speed has been determined exactly for shad, a fish showing a TMR; Leggett and Trump

1978). The fact that sea hares and migratory birds show a TMR suggests that the advantage accrued from the TMR outweighs the disadvantage of not always swimming at a constant, energetically-optimal speed. Perhaps the TMR enables more exact measurement of water current or wind direction over a range of current or wind aspects, by an as yet unidentified method. Such information about the surrounding medium would certainly have adaptive value to a goal-directed migrant.

The Migration Question

For sea hares, swimming is clearly an effective means of local movement when near land, and not just an escape response from benthic predators, as is the case for most other opisthobranchs. The sensory capabilities and some of the orientational guideposts used by sea hares in shallow water should also be available when they are swimming farther from shore, as would be the case during a migration. If sea hares swim when tidal currents are minimal or flowing in an advantageous direction, long distance movements could occur.

The suggestion that sea hare abundance in shallow water peaks during the spring is based primarily on records of animals stranded on beaches. Because subtidal grassbeds in shallow water have not been sampled rigorously (Hamilton et al. 1982), an alternate explanation exists for the spring peak in stranding, which does not involve migration: Populations of sea hares in subtidal grassbeds may be seasonally stable, but swimming (and thus stranding) may only occur in the spring.

Two arguments oppose this alternate explanation. First, the diversity and abundance of macroalgae associated with grassbeds is great in the winter but decreases strikingly by the summer (Phillips 1960; Dawes 1974, 1983, personal communication). This algal bloom would comprise an attractive food source for spawn-producing adults, a more cryptic environment for egg mass protection, and a favorable growth environment for newly settled juveniles. Gev, Achituv and Susswein (1984) note that "the *Aplysia* season" in shallow water coincides closely with the period of peak algal abundance. Second, summer water temperatures in the shallow bays of southwest Florida often exceed 30°C, and 39°C has been recorded (Philips 1960). Sawaya and Leahy (1971) reported that sustained exposure of *A. brasiliana* to water at 27°C is almost always fatal, and Ambrose (unpublished) found that exposure to 31°C was fatal within 24 hrs. Sawaya and Leahy speculated that *A. brasiliana* migrate to deeper water when shallow water temperatures become high. Many other marine and freshwater molluscs (and other animals) undergo annual migrations to and from shallow water in avoidance of temperature stress (see examples above and Gauthreaux 1980). In summary, the same southwest Florida grassbeds whose algae provide an abundant source of nutrients for conversion into eggs in late winter and a favorable growth environment for newly settled juveniles during spring are less hospitable to sea hares during summer. Therefore, it seems quite unlikely that sea hare populations in shallow-water grassbeds are seasonably stable.

I suggest that ***Aplysia brasiliana*** undergo an annual migration between deep and shallow water in southwest Florida. The deep water habitat could be farther offshore within the bay system, or out in the Gulf of Mexico. ***Thalassia*** grassbeds are not usually found deeper than about 2 to 3 m in bays (because of turbidity) but reportedly occur at depths exceeding 20 m in the Gulf of Mexico (Dawes 1974). ***A. brasiliana*** have been collected in the Gulf at a depth of 13 m (Tunnell and Chaney 1970), and other ***Aplysia*** species occur to depths of 30 or 40 m (Marcus 1972). I have collected stranded ***A. brasiliana*** on the Gulf of Mexico side of a barrier island from beaches located farther than 8 km from any pass connecting the Gulf to protected waters behind the island.

PROSPECTUS

Our understanding of orientation and migration in molluscs is limited. Very little is known about subtidal species and, even for intertidal molluscs, hypotheses about underlying orientational mechanisms and adaptive values rarely have been tested.

Many migrations claimed for molluscs are based only on inferences drawn from population sampling, and this has led to controversy about whether some of the speculated migrations actually occur. Direct evidence in the form of movement records of tagged individuals needs to be obtained for many species, including ***Aplysia***. Shelled species can be tagged easily by various methods. The freeze-branding technique used on terrestrial slugs (Richter 1976) may work for some of the shell-less opisthobranchs. Heat branding works well for ***Aplysia***. Sonic tracking has been used only rarely for molluscs (Clifton, Mahnken, Van der Walker and Waller 1970; Auffenberg 1982; Mather, Resler and Cosgrove, in review) and this technique could be used more extensively as very small transmitters are now available.

The oriented movements of many gastropods have been attributed to simple phototaxis or geotaxis, or to chemodetection of mucous trails. However, research on ***Littorina irrorata*** and ***Aplysia brasiliana*** suggests that the orientational strategies and sensory worlds of some molluscs are considerably more complex. Molluscan ethologists must recognize that many animals use a hierarchy of orientational guideposts for homing or migration; elimination of only one potential guidepost at a time in experimental studies can lead to erroneous conclusions if involvement of only one guidepost is assumed.

Finally, molluscs are a very diverse group with a long geologic history, so conclusions about orientational mechanisms or adaptive functions for particular movements should be extrapolated across species cautiously. Many swimming methods exist within the opisthobranchs (including at least four within just the Aplysiidae) and the role of swimming may vary among species. Homing behavior has evolved independently at least four times, so the guideposts used by one species may not be the same ones used by all others. Visual capacities of gastropods range widely, even within a single genus such as ***Littorina*** (Hamilton, Ardizzoni and Penn 1983), so making generalizations about the role of vision in gastropod orientation is

risky. Behaviors of many molluscan species must receive thorough and unbiased analysis if valid conclusions about the entire group are ever to be reached.

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ADAPTIVE SIGNIFICANCE OF SHORT-RANGE DIEL MIGRATION DIFFERENCES IN A SEAGRASS-MEADOW SNAIL POPULATION

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ABSTRACT

Behavioral changes during an animal's migration and in corresponding experiments can indicate selection pressures that alternate in importance during the migration. ***Anachis avara semiplicata*** snails in seagrass meadows migrate daily up and down seagrass blades. The snails move up at night and graze areas of epiphytic algae on the blades; they return to dense cover in bottom refuge areas during daylight. Repeated exposure to each algal substrate on the seagrass blades leads to the accumulation of that substrate material on snail shells. Bare shells appear to match the mud bottom, where experimentally transferred shells lose their algae. Large adult snails of ample age to be coated with algae showed long-term differences in the types of algae coating the shell. Laboratory and field analyses showed that the ***Anachis*** snails were very mobile among various substrata at night. Yet individuals without algae on their shells tended to occur among mud patches during daytime and to move only ca. 10 cm up seagrass blades at night. Two additional shell categories had coralline or filamentous algae on their shells, and tended to migrate ca. 20 cm up shoalgrass or turtlegrass blades. At dusk the latter phenotypes emerged from being hidden at the bottom and moved high up onto the particular seagrass species whose algal overgrowth matched their shell overgrowth. Female ***Anachis*** laid their eggs on turtlegrass blades near the base, yet bare snails and individuals with coralline algae coating the shell showed very similar sex ratios.

Various fishes and bluecrabs (***Callinectes sapidus***) are significant predators on ***Anachis***. The presence of such predators in this study caused snail distributions to shift to the bottom. An hypothesis is derived that such predators provide selection pressures favoring movement of individuals in one of several different migration patterns (i.e., long migrations up the seagrass blades in the case of algae-covered snails, or very short vertical movements for bare-shelled snails). Each migration pattern appears to provide a thoroughly hidden refuge by day and a particular appearance for crypsis, either on the bottom or up among their preferred algal foods. Analogous selection pressures appear to influence many diel migrations.

INTRODUCTION

In the marine environment, vertical migration has been studied most extensively with various zooplankton. Angel (this volume) describes zooplankton migrations through marked depth gradients of predation pressure and food; such movements often appear to facilitate avoidance of visual predators during daylight hours, yet provide a means to reach appropriate food resources when the risk of visual predation is diminished.

As with vertical migration over large depth gradients by zooplankton, shorter diel movements of benthic animals may be a response to opposing selection pressures; benthic migrants may avoid visual predators by day, yet permit grazing at night on palatable foods in exposed locations. Such opposing selection pressures for hiding versus feeding during diel migrations are noted by Alldredge and King (1977) and Bell, Walters and Kern (1984). These authors describe migrations of potentially planktonic animals that often occupy the bottom by day.

The study described below presents an example of an apparently similar phenomenon among bottom-dwelling gastropod browsers, ***Anachis avara semiplicata***, in a shallow seagrass community. ***Anachis*** shows a feeding preference for epiphytic algae that cover upper seagrass blades (Kitting 1984). The snails appear to move out along the blades at night for foraging. The downward or return migration at dawn is thought to be a response to visual predators. Evidence for the latter hypothesis includes the observation that the snail's distribution on the seagrass blades shifts downward in the presence of predators; previous reports also suggest that seagrass meadows provide densely concentrated small animals with a refuge near the bottom, protected from larger predators (Heck and Orth 1980; Stoner 1982; Orth, Heck and van Montfrans 1984). Furthermore, two groups of individuals in the study population, which show different degrees of crypsis, are seen to differ in the distance that they migrate.

Direct, in situ, close-up monitoring methods used in the present study are sometimes the most practical way to quantify behaviors of individuals repeatedly without disturbance (after Hermkind 1974), even when the behaviors are hidden from view. Kitting (1979, 1984) has shown that easily distinguishable sounds of small molluscan browsers correspond to (1) differences among consumer species (due to different mouth parts and feeding behaviors), (2) different ***foods***, distinguished by different textures and consistencies of algal foods, and (3) location and time of feeding. One can quickly learn to recognize the distinctive sounds through simulation of feeding or other behavior with forceps. Such studies can also expand our perception of other periodic behaviors of organisms, such as scraping of the shell during movement or periods of no such activities at all.

MATERIALS AND METHODS

The study area is several kilometers from Gulf passages into Redfish Bay, near Corpus Christi and Port Aransas, Texas (27°50′N, 97°5′W). Redfish Bay and surrounding bays average 1−2 m in depth, are several kilometers wide, have little wave action, tide, or current and have five species of seagrasses in roughly adjacent patches. At Redfish Bay the major species of seagrass is turtlegrass ***Thalassia testudinum***. The most common animals include the gastropods ***Anachis avara semiplicata*** (200·m^{-2}; 1 per blade) and ***Bittium (Diastoma) varium*** (2000·m^{-2}; 20 per blade). Ecological aspects of local bays have been studied extensively by Hedgpeth (1947) and Odum and Wilson (1962).

Quantitative field observations were conducted primarily from July through November 1981−3, when gastropods were especially numerous. In situ, time-lapse, underwater photographs were made with a remotely triggered motor-driven camera and a flash in underwater housings. A remote timer enabled automatic photographs at 16-min intervals. The resulting color transparencies were scored on an eyepiece grid by viewing the transparencies with diffuse transmitted light on a stereo microscope at 10×−20× magnification.

Traditional methods such as direct observations of small animals are very limited for quantifying animal behaviors during slow migrations. Common, slow-moving animals (especially molluscs) are often hidden from view, and lights can be a major disturbance. I developed close-up listening methods as a promising solution, and they sometimes prove very useful for quantifying hidden foraging behaviors (Boyden and Zeldis 1979; Kitting 1979, 1980; Kitting, Fry and Morgan 1984). Rather than the usual, pooled data on groups of individuals, repeated sampling is possible for each individual without much disturbance. The underwater camera was aimed at four underwater contact hydrophones (Sound Wave, of Micro-Communications, Santa Ana, CA). Microphones were anchored on the sediment and blades with wooden clothespins. Readily available electric components were used, including Sony D5M and WMD6 stereo cassette recorders. When feeding occurs near the hydrophone, one can often determine when and where (and generally what) each individual organism is eating. Tapes of such distinctive feeding sounds have been compared successfully to feeding behavior and confirmed with stomach analyses. After initial starvation and clearing of the gut, analyses of the empty stomachs of quiet individuals demonstrated virtually no inaudible feeding even on detritus; simulated feeding disturbances, produced with a probe, confirm that even delicate motion is audible quite clearly with contact microphones (e.g., Kitting 1979, 1984).

Concurrent photographic samples, as time-lapse color transparencies, were surveyed with a stereo microscope. Positions of animals were traced through time and compared to the recordings of feeding noises. These tabulations quantified changing distributions of the snails and their corresponding feeding occurrences. Periodic sounds from the camera's shutter and motor kept the data synchronized. Data from different time periods were tabulated separately. Most algae were concentrated at the blade tip, and dense dead blades and detritus were near the bottom. Therefore the

data can reflect movement and feeding among algae up on the blades versus such activities among the dense detritus and dead blades on the bottom.

Over 20 individual snails were marked conspicuously in order to follow them in dense seagrass cover beyond the 24-h photographic coverage. A 5-cm length of monofilament fishing line was striped distinctively with durable fingernail polish topped with a reflective "sequin" and epoxy-cemented out from the posterior end of each snail shell. It provided a "whip antenna" trailing out from under most forms of cover and introduced minimal obstruction to the snail's movement, as viewed in aquaria and in the field. Red filters (Kodak #29 gel) placed in underwater lights minimized disturbance during direct observations.

A laboratory experiment compared algal recruitment onto living versus dead ***Anachis*** shells. Eight live snails and 8 empty shells were cleaned thoroughly and placed in aquaria with coralline algal cultures on the walls. Empty shells were cemented onto aquarium walls with underwater epoxy cement. Live ***Anachis*** were dabbed with cement to control for any effect of cement, but were allowed to move throughout the aquarium. After 3 weeks, coralline algal colonists on the shells were enumerated in 2 × 2-mm fields under a dissecting microscope.

Further observations of ***Anachis*** distributions were conducted with and without predators in three laboratory aquaria (50 l each) with freshly collected ***Thalassia*** sod and flowing seawater at ambient conditions (27°C). An LD 12:12 light cycle under fluorescent bulbs, provided 100 $\mu Ein \cdot m^{-2} \cdot s^{-1}$ of light to the bottom, as in the field. Ten ***Anachis*** of each of two phenotypes (coralline algal-coated and uncoated shells) were added to each aquarium and allowed to acclimate for ≥ 24 h. Each aquarium was then stocked with either three 10-cm wide bluecrabs (***Callinectes sapidus***), three 10-cm long toadfish (***Opsanus beta***), or with no predators (as a control). Numbers of each phenotype on the bottom or blades were then tabulated at 2-h intervals overnight (1700−0300 hrs). On subsequent nights, predators were transferred among tanks and left for ≥ 24 h before further tabulations of snail distributions. Such substituted treatments thus standardized availability of substrata while minimizing any effects of different turtlegrass sod or snail populations and left predation as the experimental variable. Tabulations were thus based on three aquaria for each predator species or control.

Finally, a similar field experiment was conducted in the natural environment of a shallow (0.5-m deep) turtlegrass meadow. Paired cages 1m × 1m × 0.7-m high were made with polyester "double-knit" fabric sewn loosely around steel frames that were coated with nontoxic epoxy paint. Cages were anchored down into the sod securely with wooden stakes and covered with 1 cm galvanized steel mesh to prevent bird predation. The loosely secured (unstretched) fabric enabled wave action to propogate freely through the cage, to minimize cage effects (see Virnstein 1978). An adjacent 1-m^2 area was defined between the sides of the two cages, as a partial fence open to natural predators such as fishes, crabs and birds. At 3-day intervals during this three-week field experiment, a 20-cm wide "aquarium net" was swept 10 cm above the bottom for four sweeps (1 m long) in each of the three 1−m^2 areas. After each sweep 10 cm off the bottom, a separate sweep was made along the bottom.

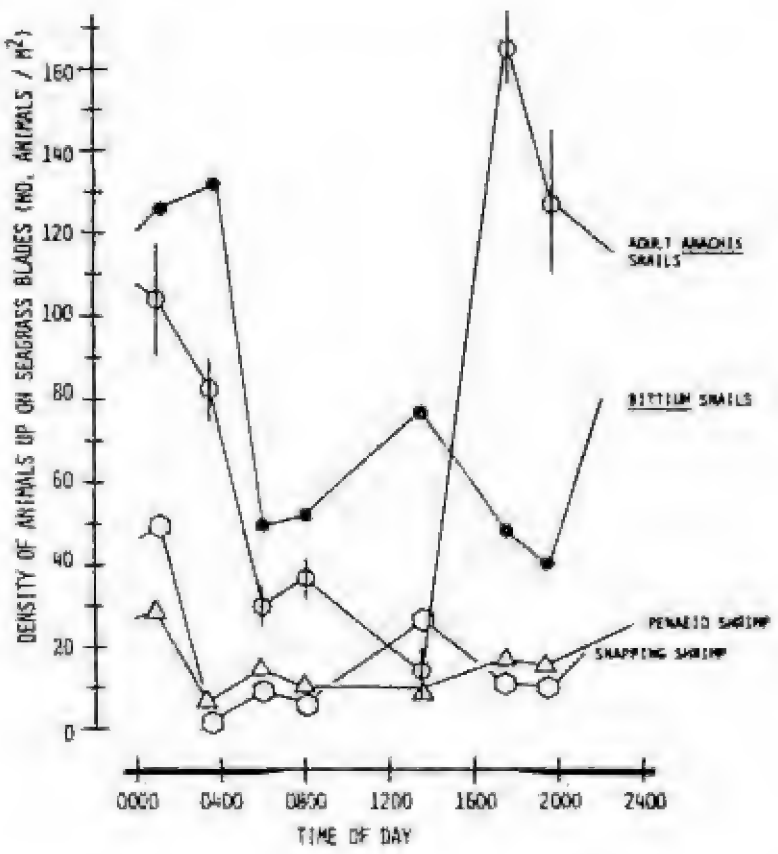

Figure 1

Summary of animal population densities observed up on shoalgrass and turtlegrass blades, throughout most of a 24 h period. Thick bar on time axis denotes darkness. Vertical bars denote standard error of sample, if larger than symbol.

Vertical distributions and relative abundances of each *Anachis* phenotype were thus tabulated for different levels of predation, being returned to their respective plots immediately after each tabulation in the field.

RESULTS AND DISCUSSION

Tabulations of snails in the time-lapse photographs from the field showed noticeable vertical migration of the snail population throughout 24 h of monitoring. The overall *Anachis* population tended to remain low on the seagrass blades or on the sediment throughout the day, but a vertically migrating portion climbed and descended a net distance of 20 cm along the blades, rising near dusk and descending near dawn an average 4 $cm \cdot h^{-1}$ along blades (Fig 1).

As the blades grow quickly from a basal meristem (den Hartog 1970), they are colonized by a variety of epiphytic organisms that build up progressively toward the (older) tip of each blade. These epiphytes begin accumulating visibly about 2 cm up the blade. Thin, flexible shoalgrass blades (*Halodule wrightii*) had frequent filamentous red algae *Acrochaetium flexuosum* and *Polysiphonia denudata*, and green algae *Cladophora* spp. (Morgan and Kitting 1984). Turtlegrass blades, which are thicker and less flexible, were covered with a lightly calcified coralline red alga *Heteroderma lejolisii* and *Spirorbis borealis* tube worms, eventually leading to a heavier coralline red alga *Dermatolithon pustulatum* near the tip. A large diatom *Rhopalodia gibberula* grew on the crustose algae and was eaten selectively with

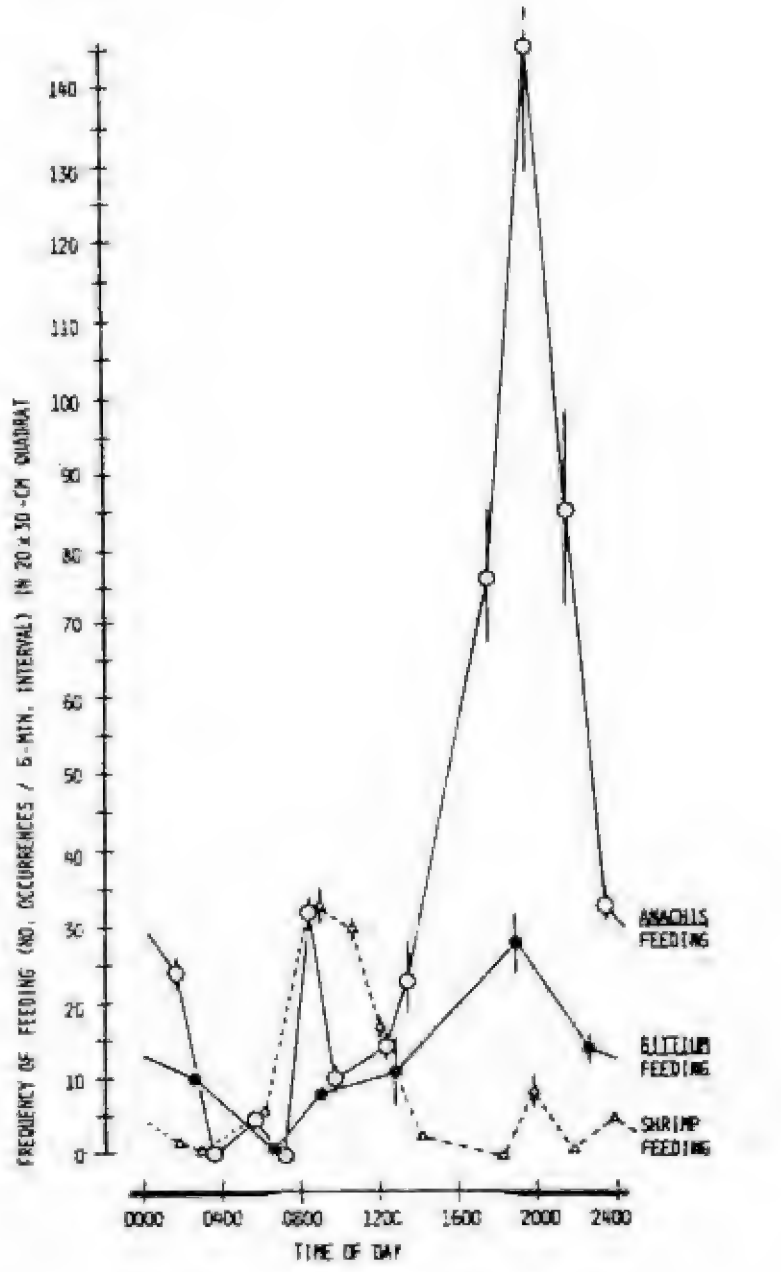

Figure 2

Feeding activities of animals sampled periodically as in Figure 1, but from hydrophones for microacoustic monitoring. Each point is based on feeding data from six, 6-min periods.

adjacent algae (Kitting 1984). These species were also found on shells of ***Anachis***. Sparse diatoms and much organic detritus and blue-green algae occur on the sediment surface. Stomach analyses of the present population showed primarily unrecognizable debris, along with various diatom species (Kitting 1984). Such dietary observations could not show when or where the animals were feeding during their migrations. Previously studied molluscs that tend to be sedentary have shown periodic migrations over rocks and include prosobranch and pulmonate limpets (summarized in Abbott, Epel, Phillips, Abbott and Stohler 1968; Cook and Cook 1981) and chitons (summarized in Burnett et al. 1975). The movements were thought to be feeding migrations in such studies, although actual feeding was usually hidden from view (Kitting 1980). Direct microacoustic monitoring in the present study showed that during ***Anachis*** migrations, feeding activity is indeed much more frequent while these snails are on the seagrass blades, particularly near dusk (Figs 1 and 2). Distinctive feeding sounds from the hydrophones corresponded to animals up on the blades during the sequential photographs and supplementary observations. Because microphones on

the bottom detected simulated and the occasional natural feeding clearly, the increased feeding frequency evident among epiphytic algae appears to be accurate; it is confirmed by laboratory analysis of *Anachis* feeding preference in which algae is preferred over detritus when both are made readily accessible (Kitting 1984).

Previous studies have reported other such diel vertical migrations among sheltered seagrasses as O_2 concentrations were depleted nocturnally at the bottom (Ledoyer 1962, 1964, 1969; Odum and Wilson 1962). The present study area is shallower and more turbulent than those investigated by Ledoyer (1962 et seq.) and Odum and Wilson (1962), and numerous other invertebrates and fishes remained near the bottom as *Anachis* (and *Bittium varium* snails) migrated upwards. It appeared very unlikely that oxygen depletion accounted for these particular migrations (Pulich, Kitting and Garcia, in preparation).

The present monitoring along with underwater observations and laboratory tests indicate that these *Anachis* select epiphytic algae rather than the detrital material commonly observed on the sediment surface (Kitting et al. 1984, Kitting 1984). The nocturnal shift up onto blades is evidently for feeding. The question arises, what is the function of the return movement?

Differences in Crypsis and Migration within the Population

At least two types of crypsis and migration occur within the adult *Anachis* population. Two visually rather distinct groups of adult snails (ca. 10 mm long) were found among turtlegrass. One generally had no macroscopic algae on the shell. The other had much of its shell covered with coralline algae *Heteroderma lejolisii* and *Dermatolithon pustulatum*. Many of the algae on the snails were reproductive, indicating significant age. Other than the algal coating, both groups appear to be morphologically indistinguishable, represent mature individuals, and have shells of ample age (ca. 1 yr) to accumulate algae. Many smaller individuals (< 6 mm long) have these algae on the shell, and adults re-acquire the algae less than 1 mo after its experimental removal. Living *Anachis* snails that were free to move among aquarium algae showed significantly greater algal growth on their shells than did adjacent empty shells that had remained stationery in the aquarium (Fig 3). Because the shell covering of *Anachis* consists of adjacent or most frequently encountered algal material, each type of shell appears cryptically colored primarily on one type of substrate: coralline epiphytes on turtlegrass, or filamentous epiphytes on shoalgrass. To the human eye, barren shells blend into the mud bottom, and algae on the shell blend in with an epiphytic alga on one of the seagrass species (Fig 4). Particularly during daytime, however, each shell type was generally hidden from view more thoroughly on the bottom, among dense and fallen seagrass blades. Since the shell covering is apparently acquired as the snails spend time on the blades, the choice of one or the other type of seagrass blade as a foraging area very likely precedes the acquisition of the cryptic covering. Such migrations out onto an appropriately matching background of algae or sediment do not require that the individual snails recognize their shell overgrowth or particular substrate; rather, a consistent migration

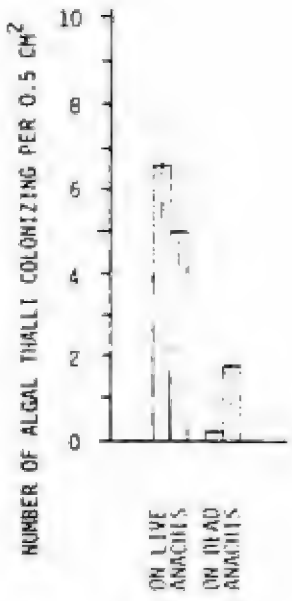

Figure 3

Algal recruitment onto living versus dead *Anachis* shells in aquaria for 3 weeks, with coralline algae on glass. Each pair of bars represents *Heteroderma* on the left and *Dermatolithon* on the right, ± 1 s.d.

Figure 4

A 60 × 90-mm view of two *Anachis* undisturbed on *Thalassia* in situ. One is cryptic on coralline algae that match the shell coating. The lower snail has a barren shell.

pattern for each individual appears to lead to the most frequently encountered algae accumulating on the individual's shell (Figs 1, 3 and 4). In the laboratory, individuals transferred to the sediment are observed to lose the algae from their shells, apparently due to abrasion and insufficient light at the bottom.

The most common shell categories among turtlegrass could be distinguished in time-lapse photographs; their movement along the blades was tabulated at 2-h intervals. Roughly similar day-night migration patterns were seen, but the coralline algae-coated individuals tended to be higher on the blades than the bare-shelled

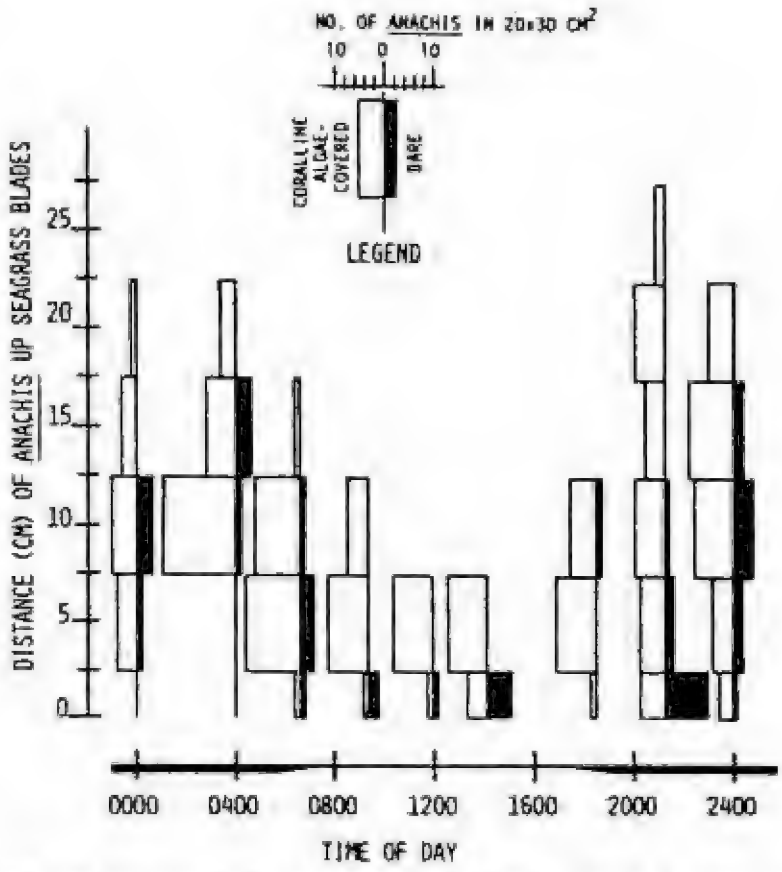

Figure 5

Distributions of each of two common phenotypes of *Anachis* on turtlegrass over 24 h. Each vertical "histogram" (analogous to a "kite diagram") represents a distribution for a ca. 2-h period. Other individuals thoroughly hidden on the bottom sediment were not quantified or plotted; on the average, they would contribute to a roughly constant total (for each phenotype) throughout the 24 h.

individuals during most of the 24-h period (Fig 5). The exception was during early morning, when observed distributions of the two were very similar (0000−0800: $G = 6.0$, 4 d.f., $0.1 < p < 0.5$; Sokal and Rohlf 1969). Their observed distributions were significantly different during 0800−1600 ($G = 77$, 5 d.f., $p << 0.005$) and during 1600−2400 ($G = 17$, 2 d.f., $p < 0.005$). Total numbers of observed individuals changed in the area photographed; bare-shelled individuals were seen less frequently during the daylight hours (Fig 5), and supplementary observations showed many individuals to be hidden on the bottom. Figure 5 shows that when snails were on the blades, the distance they moved along the blades corresponded to their shell appearance. Individual snails did not remain stationery on a matching patch but tended to move among overlapping blades at a particular height from the bottom. Qualitative observations of the very large lateral movements of individuals showed that tagged and untagged snails were moving widely at night.

Over large areas of seagrass meadows two less common groups are also found whose shells are coated with a dark, encrusting (noncalcified) alga (*Peyssonellia* sp.) or with dense diatoms and filamentous green algae (*Cladophora* spp.). Intermediate categories of shell overgrowth are also present, but uncommon. Such intermediates can be pooled with their most similar category, but illustrate that these various phenotypes all represent ***Anachis avara semiplicata*** (see Hatfield 1979).

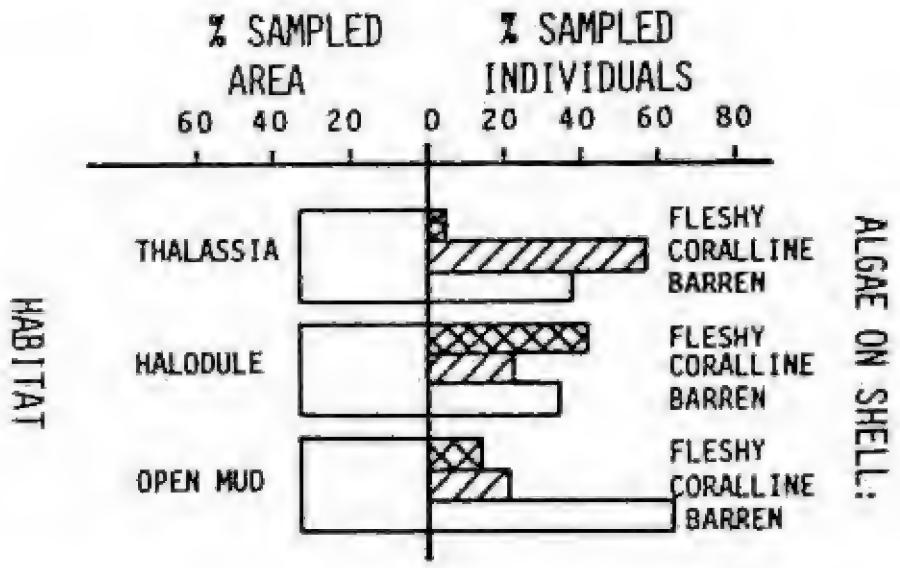

Figure 6

Frequency distributions of the three phenotypes common among *Halodule* and *Thalassia* seagrasses, and on nearby mud. *Anachis* was collected quantitatively from adjacent patches that totaled the same area (ca. 2 m^2) for each type of substrate. "Fleshy" algae were filamentous algae that grew on *Halodule*.

Anachis appeared to lay eggs at the base of seagrass blades, but sex ratios from 60 individuals with and without algal overgrowth, from upper blades versus the base, suggested no significant differences in sex ratios or size; 40% of the algae-coated (mean length 9.4 ± 1.2 mm) and 47% of the bare-shelled individuals (mean length 9.2 ± 0.8 mm) were females.

Analogous sampling of shell types in adjacent shoalgrass (*Halodule wrightii*) meadows showed that filamentous algae were very common on *Anachis* shells (Fig 6). At night these snails were usually among the filamentous algae on the *Halodule* blades. Crustose *Pessonellia*-coated individuals were too rare to demonstrate any distinctive distributions.

In the absence of the conspicuous labels on individual *Anachis*, my own observations of *Anachis* were hindered by their concealment on the bottom, and their remarkable crypsis when they were out. Similarly other visual predators appear to provide a selection pressure that would perhaps account for the daytime occupation of the bottom, and the restriction of movement primarily to their "matching" substrate.

Effects of Predators

Distributions of snails of different phenotypes were monitored in laboratory experiments in the presence and absence of common predators (toadfish and bluecrabs). Bare-shelled individuals again were on the bottom more frequently than algae-coated individuals. Actual consumption of snails by the predators was not detected, but the presence of each predator changed the distribution of the snails significantly, relative to their distribution in tests with no predators (Fig 7A; each $t > 2.0$; $p < 0.03$). In the presence of toadfish the distribution of algae-covered snails was markedly affected such that roughly half as many were found on seagrass blades when the fish were present as when they were absent. Similarly, toadfish reduced the proportion of bare-shelled animals on the grass, but the difference between the

Figure 7

A. Proportion of *Anachis* of each shell-type that occurred up off the bottom sediment in experimental aquaria. Different types of predation were present. Observations were tabulated overnight at 2-h intervals. Beginning, then final numbers of individuals observed are averaged for the replicate tests and listed at the right. No noticeable *Anachis* mortality occurred.

B. Frequencies of each shell-type that occurred on *Thalassia* blades in field plots. Predators were excluded from two plots, and two plots were open to predators. Observations were tabulated at 3-day intervals for 3 weeks. Beginning, then final numbers of individuals per sample, averaged for replicate samples, are listed at the right. Sampling variability appeared larger than any overall prey depletion during the experiment.

distribution in the presence and absence of fish was less for bare-shelled than for algae-covered snails (Fig 7A). Thus in spite of their cryptic coloration, algae-coated snails were clearly affected by the presence of toadfish. Bluecrabs caused a similar shift to the bottom in bare-shelled snails but had less effect on algae-coated individuals (Fig 7A). Direct observations suggested that snails were being dislodged as the predators moved among them. Tests with each type of predator shared the same available areas of each substrate, as use of aquaria rotated (see methods). Repeated observations indicated that virtually no exposed individuals were being overlooked by the observers, although snails were often very cryptic.

In the analogous field test with periodic observations (not strictly independent), individuals were distinguished as bare-shelled, completely coated with coralline algae, or partially coated. Composition of the population on the blades differed between plots with natural versus decreased predator access (Fig 7B, $G = 9.8$, $p < 0.05$). In the presence of predators, bare-shelled and fully coated snails were shifted further onto the bottom as in the laboratory experiment, but surprisingly, snails only partially coated with algae were more frequently seen on the blades in the presence than in the absence of predators, possibly because attempted predation resulted in the removal of shell algae.

Three major groups of predators are commonly active in such shallow-water communities: birds, fishes and crabs. Barrass and Kitting (1982 and in preparation) summarize the sparse data available on the influences of avian predators on seagrass-meadow invertebrates and show experimentally that bird activities can change distributions of small crustacea more than expected from actual minor consumption of the prey; a variety of invertebrates may similarly flee such disturbance by predators. Human pursuit of ***Anachis*** caused disturbed snails to fall to the bottom as did disturbance by predators. Such activity sometimes caused algae to be chipped off the shell. Other would-be predators appear to cause such shifts in distributions. Common, aggressive pinfish (***Lagodon rhomboides***) or bluecrabs (***Callinectes sapidus***) have been kept in field enclosures where invertebrate distributions were compared with control enclosures; undisturbed invertebrates were up among seagrass blades more frequently than when disturbed (Huh 1983; Eldred, in preparation). Various fishes (Adams 1976, Nelson 1981, Livingston 1982) and crabs (Hamilton 1976, Orth 1977, Heck and Thoman 1981) are known to prey on local snail species. ***Callinectes sapidus*** may affect prey ***distributions*** even more than prey abundances (Young, Buzas and Young 1976; Barrass and Kitting, in preparation).

Analogous invertebrate migrations out into the open at night are reported from similar environments for other seagrass invertebrates (Ledoyer 1962, 1964, 1969; Greening and Livingston 1982) such as sea urchins (Kempf 1962), grass shrimp (Hubbs and Velderman 1968), subadult lobster (see Lipcius and Herrnkind 1982) and meiofauna (Bell et al. 1984). The roles of coloration and predation in such diel migrations are reviewed by Angel (this volume) who notes that organisms from plankton to mammals often show close relationships between their coloration, habitat shifts, and periods of visual predation. Lee (1965) has presented one of the few such examples studied physiologically and ecologically: a marine isopod that spends a period of its life on seagrass and obtains its cryptic coloration from its substrate after a long migration from other, algal substrata.

The distance that ***Anachis*** migrates up the blade corresponds to its shell appearance. Analogous examples of individually different distributions and crypsis are suggested for limpets on different backgrounds (Giesel 1970) and for nudibranch and ovulid molluscs that accumulate pigmentation from their diets of hydroids (Harris 1973) and sea-whips (gorgonacea; Chapter 3 in Fotheringham 1980). Kellogg (1980) uncovered evidence that certain nudibranchs may avoid fish predators largely through such matching coloration which can sometimes change when an animal moves to a

new patch of food and incorporates new pigments from that food (Harris 1973).

An additional adaptive significance of such an acquired camouflage in a particular microhabitat is that it may function chemically even in darkness. Fishlynn and Phillips (1980) showed that the shell of a seagrass-dwelling limpet accumulates compounds from the seagrass where it is less recognizable by chemically sensitive predatory starfish. Vance (1978) showed analogous temporary chemical camouflage by scallops that avoided seastar attack after acquiring overgrowth of surrounding sponges. Even when predators such as bluecrabs are foraging with chemotaxis, algal overgrowth of snails may provide such chemical camouflage.

My observations on *Anachis* foraging migrations suggest the importance of two opposing selection pressures: requirements for foraging versus protection from associated predation (or other possible risks of daylight hours, such as excessive heat in summer months). Previous seagrass meadow research has shown active disagreement about the relative effects of food versus predators in these very dense concentrations of small animals in various seagrass meadows. One can hypothesize that food requirements influence the change in distributions of small animals at night, but large visual predators (or other daytime hazards) favor migrations of such vulnerable animals down into more protected microhabitats during daylight.

Future studies may test such a broad hypothesis further. One can consider migrating plankton vulnerable to small fishes (cf. Zaret and Suffern 1976; Enright 1977; Robertson and Howard 1978; Tranter, Bulleid, Campbell, Higgin, Rowe, Tranter and Smith 1981; Bird and Kitting 1982), demersal or benthic invertebrate migrations (e.g., Alldredge and King 1977), or a variety of other animals in terrestrial, aerial, or marine environments. It is becoming clear that diel or other migrations can, in response to opposing selection pressures, provide the "best of both worlds": the alternation of microhabitats suitable for feeding and then hiding during the diel period.

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DIRECTIONAL MOVEMENT IN A SEA STAR (*OREASTER RETICULATUS*): ADAPTIVE SIGNIFICANCE AND ECOLOGICAL CONSEQUENCES

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ABSTRACT

The sea star *Oreaster reticulatus* is a microphagous grazer on sand and seagrass bottoms in the Caribbean. Foraging paths of *O. reticulatus* are directional and the distance traveled between feedings generally approximates the sea star's diameter. This movement pattern prevents overlapping feeding sites and minimizes foraging effort on homogeneous substrata.

In a large sand patch amid a sea grass bed, *O. reticulatus* formed dense aggregations which migrated throughout the patch in protracted grazing fronts. Frontal movement was directional; fronts were retracted and deflected at the seagrass border. Intense feeding activity within a front resulted in a rapid turnover of sediment and a marked decrease in benthic microalgae. Sea stars foraging in the wake of a front, where food was scarce, moved greater distances than those within the front. When translocated from the sand patch to the surrounding sea grass bed, *O. reticulatus* homed towards aggregations of conspecifics in the patch. This behavior would enable sea stars to locate and remain within preferred habitats and may account for the high density of *O. reticulatus* in isolated sand patches.

Directional foraging movements, mass migration, and homing behavior have been documented in other species of sea stars in relation to habitat preferences and food supply. Although the adaptive significance of such movement patterns seems clear, the orientational mechanism(s) are poorly understood.

INTRODUCTION

Sea stars are active foragers and may move considerable distances, albeit slowly. However, information on sea star movements and migrations is largely anecdotal (see reviews in Feder and Christenson 1966, Sloan 1980); few studies have analyzed movement patterns (Burla, Ferlin, Pabst and Ribi 1972; Ferlin 1973; Pabst and Vincentini 1978; Thompson and Thompson 1982).

In this paper, I present an overview of my studies of movement and migration in a tropical sea star *Oreaster reticulatus* (Scheibling 1979, 1980a,b, 1981a). I consider the adaptive significance of foraging movements in the context of optimality theory, and discuss possible orientational mechanisms underlying directionality of movements.

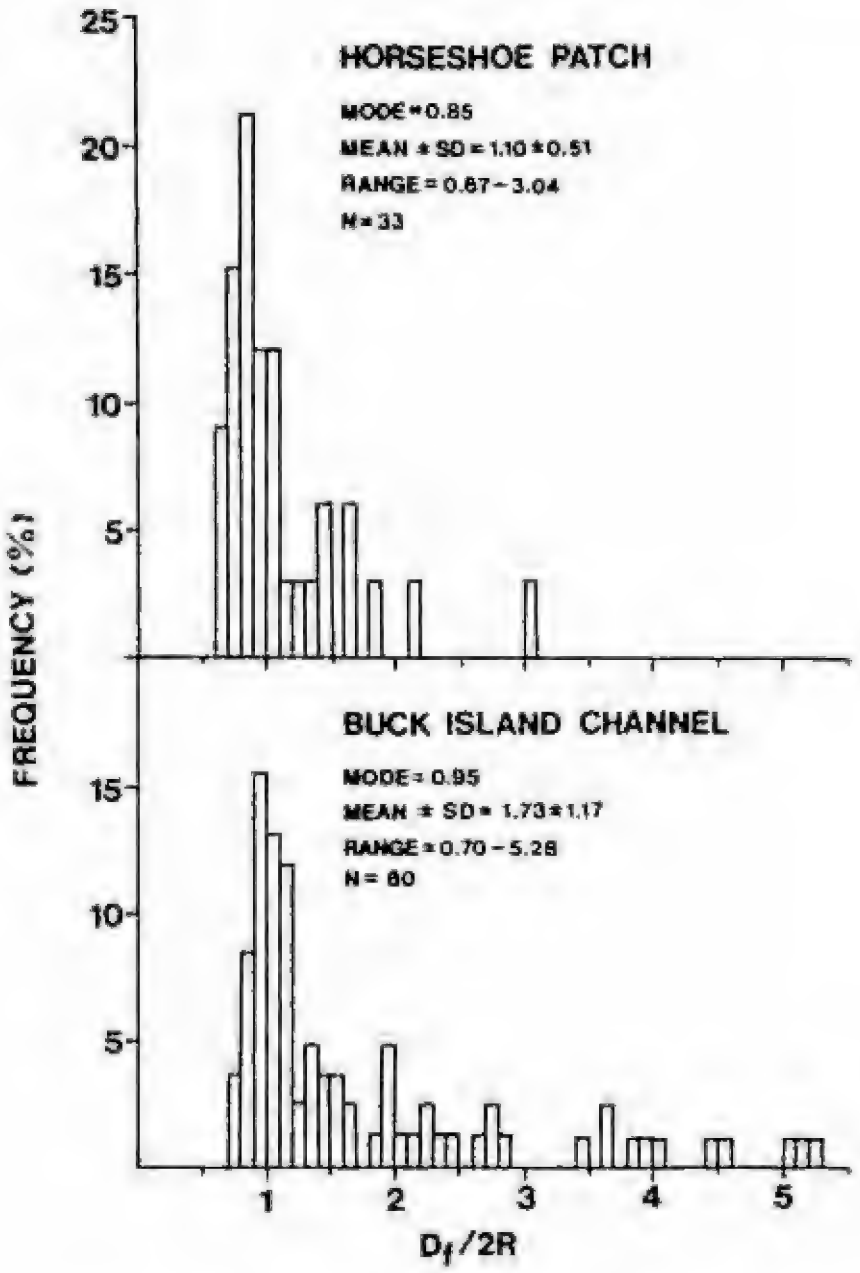

Figure 1

Frequency distributions of the ratio of interfeeding distance-to-diameter ($D_f / 2R$) of *Oreaster reticulatus* in Horseshoe Patch and Buck Island Channel (from Scheibling, 1981b).

I also examine feeding migrations and homing in *O. reticulatus* and other sea stars, and the ecological consequences of these behaviors. I hope to show that despite their lack of cephalization, central nervous organization and complex sensory structures, sea stars are capable of directed movement. Indeed sea stars may be useful models for evolutionary/ecological studies of marine invertebrate movement patterns and migratory behavior.

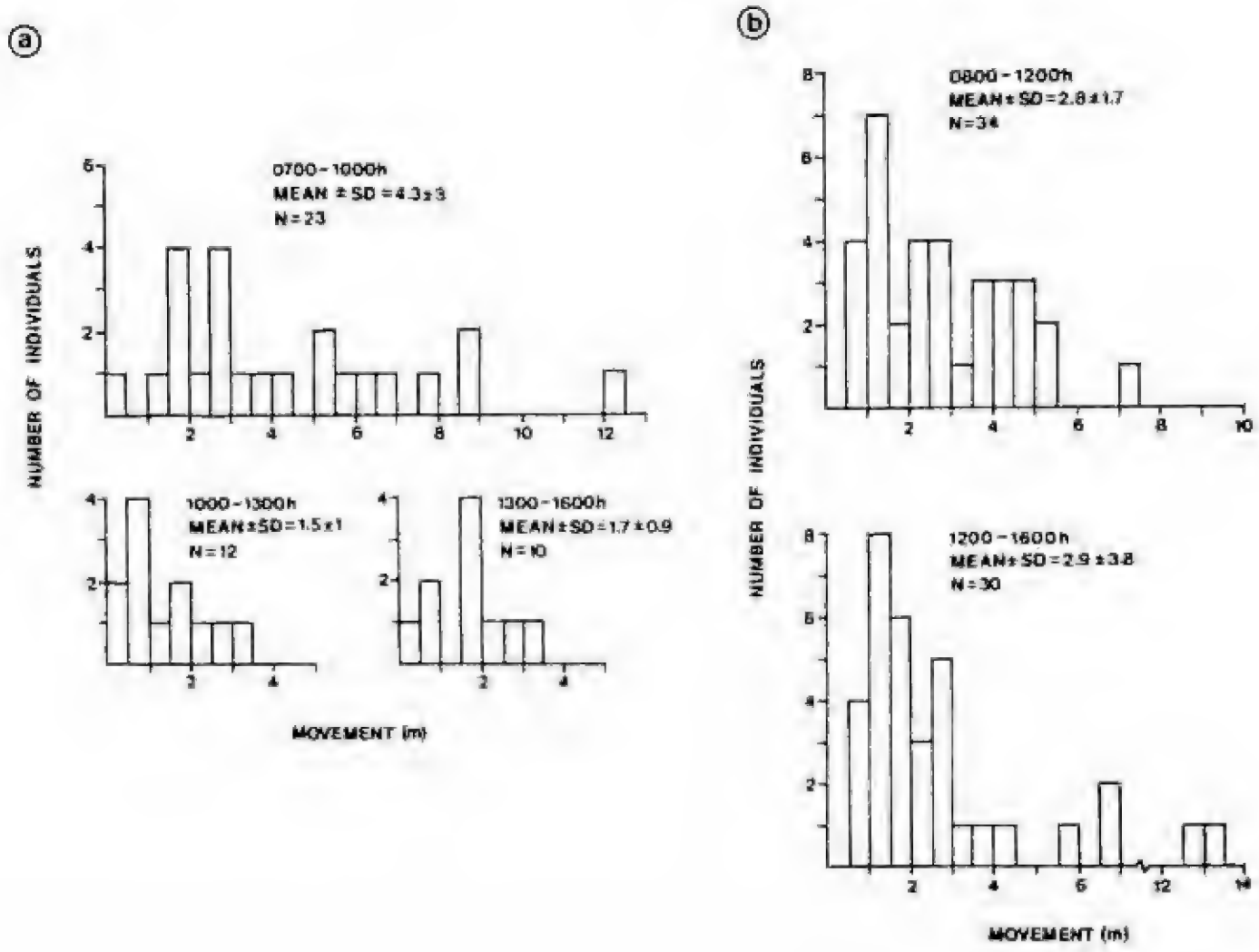

Figure 2

Frequency distributions of distances moved by *Oreaster reticulatus* in (a) Horseshoe Patch during 3-h intervals, (b) Buck Island Channel during 4-h intervals.

FORAGING MOVEMENTS OF INDIVIDUALS

Oreaster reticulatus is an omnivorous grazer of microorganisms and detritus in shallow sand and seagrass habitats in the Caribbean (Scheibling 1982a). Movement patterns of foraging individuals were studied using SCUBA at two sites off St. Croix, U.S. Virgin Islands: Horseshoe Patch, a large sand patch (30,500 m^2) surrounded by dense seagrass beds; and Buck Island Channel, an extensive sand plain. The sand substratum of each area was relatively homogeneous in terms of grain size and organic content (Scheibling 1980c). Depth ranged from 10−13 m in both areas. Individual sea stars were marked by scarification and their movements measured with references to fixed point or grid systems on the bottom (Scheibling 1979, 1981a). Foraging paths were clearly demarcated by a series of sediment mounds indicating successive feeding sites.

The average distance traveled by ***Oreaster reticulatus*** between successive feeding sites (interfeeding distance, D_f) was positively correlated with individual size (measured as radius, R). To compare movements of individuals differing in size, interfeeding distance was expressed relative to sea star diameter by the ratio, $D_f / 2R$. Frequency distributions of $D_f / 2R$ in Horseshoe Patch and Buck Island Channel are

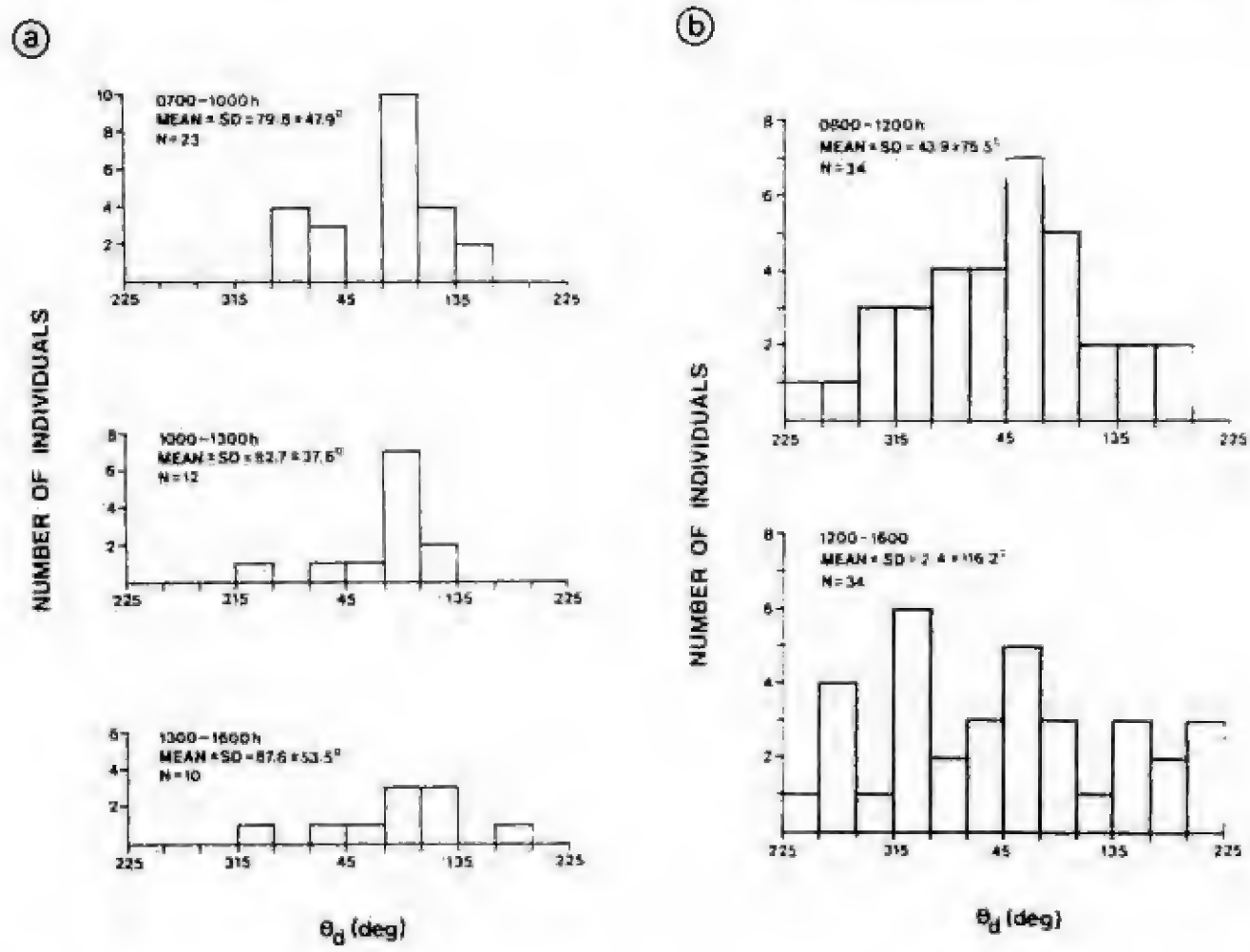

Figure 3

Frequency distributions of the direction of movement (θ_d) of *Oreaster reticulatus* in (a) Horseshoe Patch during 3-h intervals, (b) Buck Island Channel during 4-h intervals.

unimodal and skewed to the right (Fig 1). The mode approximates unity, indicating that sea stars most frequently moved a distance equivalent to their own diameter between successive feeding sites. Average ratios of the net distance moved (distance between initial and final feeding sites, D) to total distance moved ($\sum D_f$) during 3 to 4-h periods of observation were 0.82 in Horseshoe Patch and 0.93 in Buck Island Channel, which indicated that foraging movements were highly directional. This observation was substantiated by in situ observations of moving sea stars and the trails made by their tube feet between feeding sites.

To examine movements over longer periods, successive positions of individual sea stars were recorded at 3 or 4-h intervals in each study site. Frequency distributions of net distances (Fig 2) and directions (Fig 3) moved per sampling interval, and of angular differences in direction of movement between successive intervals (Fig 4), indicate that *Oreaster reticulatus* maintains a pattern of limited and directional movement over 8- to 9-h periods of continuous foraging-feeding activity. The average movement in each study site (measured over successive intervals) was 6–7% of the estimated maximum movement theoretically possible on the basis of average locomotion ($\approx$ 20 cm·min^{-1} on sand). Non-uniform distributions of angular differences in direction of movement between successive intervals (Fig 4) indicate directional movement: 100% and 87% of individuals deviated $< 90°$ in Horseshoe Patch and Buck Island Channel, respectively. The average angular deviation did not

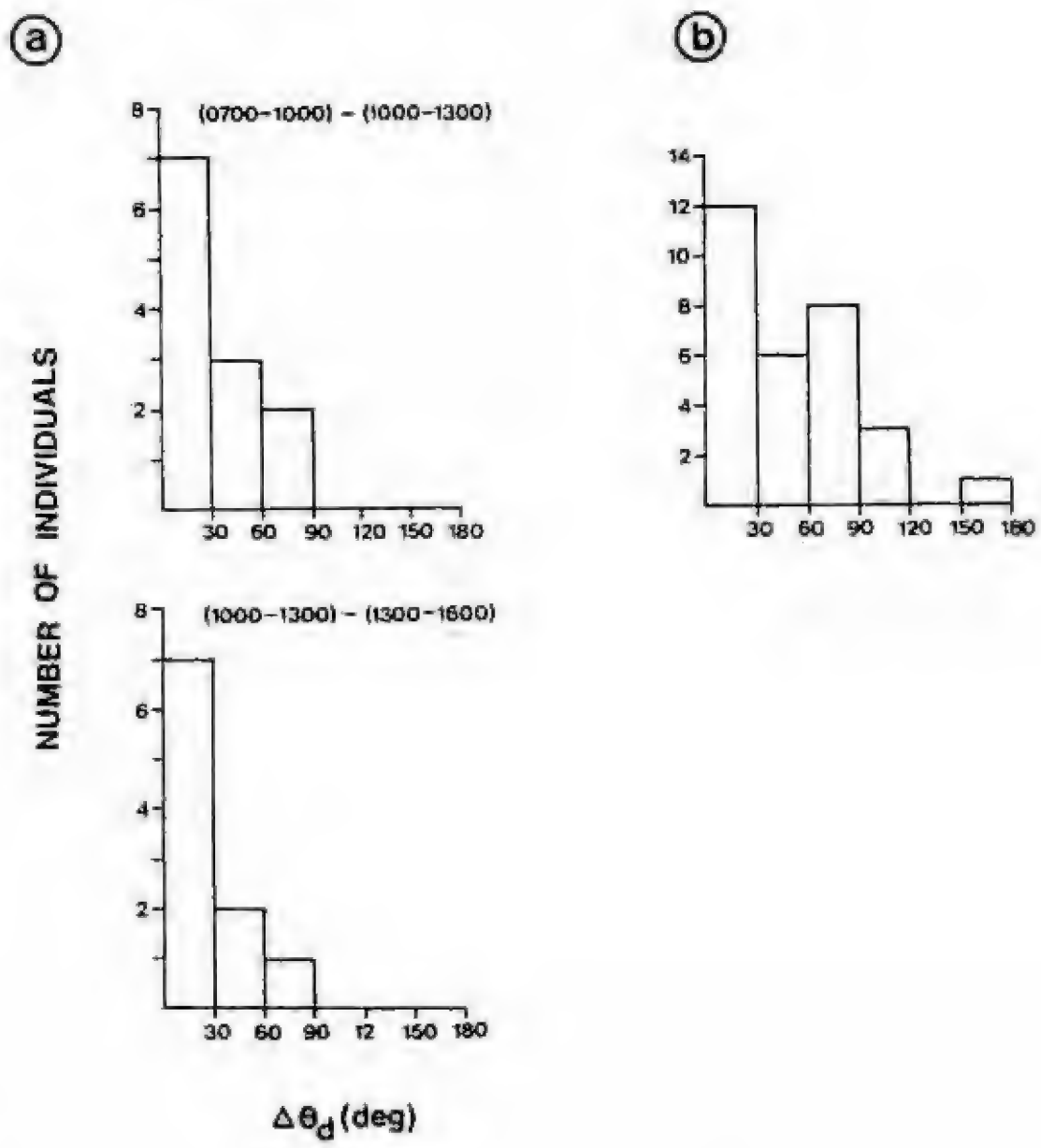

Figure 4

Frequency distributions of angular differences in the direction of movement ($\Delta\theta_d$) in (a) Horseshoe Patch between 3-h intervals. (b) Buck Island Channel between 4-h intervals.

differ significantly from 0° (unidirectional movement) between successive intervals at each study site.

In Horseshoe Patch, the distributions of directions of movement (Fig 3a) were significantly nonrandom and the average direction of movement was relatively constant throughout the day (it varied < 5° between successive intervals), reflecting a mass migration of sea stars across the sand patch. This migratory behavior culminated in the subsequent formation of dynamic "fronts" of sea stars in Horseshoe Patch (see below). In Buck Island Channel, the distribution of directions of movement (Fig 3b) was significantly nonrandom in the morning but random in the afternoon. It was also random for movements measured over 24 h. Occasional periods of randomly oriented foraging movements, and/or directional changes between activity periods, may account for the generally random spatial distribution of sea stars in Buck Island Channel.

ADAPTIVE SIGNIFICANCE

The pattern of foraging movements of a predator is an integral component of its feeding strategy. Optimal foraging theory predicts that natural selection will favor behavioral patterns which maximize the net rate of food (or energy) uptake (Krebs 1978). To assess whether observed foraging movements of ***Oreaster reticulatus*** optimize feeding efficiency, we need to consider both the sea star's feeding mechanism and the distribution of its food resource.

Upon locating a feeding site, ***Oreaster reticulatus*** uses its tube feet to rotate about its central axis while simultaneously raking the organic-rich surface layer of sediment toward the mouth. The resultant sediment mound is enveloped by the everted stomach and particulate organic matter is ingested. Thus ***O. reticulatus*** draws upon a circular area defined by its diameter while feeding (Scheibling 1980e). By moving a distance approximating its diameter between feeding sites, ***O. reticulatus*** minimizes time and energy spent in foraging. For example, during continuous foraging feeding activity, sea stars feed at a different site approximately once every hour (Scheibling 1981a). Time spent in moving between feeding sites (search time) and in accumulation (handling time) represents approximately 5% and 15% of each hour, respectively, leaving 80% of the time for feeding.

Overlap between feeding sites, when it occurs, is generally minimal relative to the total area of the site (7% and 1% in Horseshoe Patch and Buck Island Channel, respectively). Extensive overlap would decrease feeding efficiency since ***Oreaster reticulatus*** markedly reduces food resources within the feeding site (Scheibling 1980e).

Minimal foraging movements are clearly optimal for a microphagous grazer when the distribution of its food resource is continuous and uniform. These conditions are approximated on homogeneous sand bottoms. Measurements of chlorophyll and total organic content of sediments in both study sites (Scheibling 1980c,e) indicate a relatively uniform horizontal distribution of microalgae and organic matter. Of course, sea star grazing in itself imposes patchiness. (This may become pronounced when sea stars form migratory fronts as in Horseshoe Patch.) In areas undisturbed by sea stars for several weeks, an even microalgal-detrital film was visible on the substratum.

I have hypothesized that feeding activity in ***Oreaster reticulatus*** may be triggered by chemoreception of organic material in the sediment (Scheibling 1981a). This may involve the summation of stimuli transmitted via sensory receptors on the tube feet. If the sediment is rich in organic material, the threshold of the feeding response may be reached before an individual has completely withdrawn from the previous feeding site, resulting in partial overlap of sites. Alternatively, if an individual encounters a patch of low organic content (perhaps due to grazing by conspecifics) it may travel a distance several times its diameter before locating a suitable feeding site.

Directional foraging movement may increase foraging efficiency by preventing an individual from re-encountering an area it has recently grazed. Directional foraging movements have been reported in other sea stars: ***Astropecten*** species on sand bottoms (Burla et al. 1972, Ferlin 1973, Pabst and Vincentine 1978) and ***Linckia laevigata*** on coral reefs (Thompson and Thomson 1982).

ORIENTATION MECHANISMS

Studies of Buck Island Channel demonstrated the ability of ***Oreaster reticulatus*** to move in approximately unidirectional but variably oriented foraging paths. Such paths also have been documented in ***Linckia laevigata*** on a coral reef (Thompson and Thompson 1982). The orientational mechanism(s) underlying such directional movement is unknown. Some species of sea stars have been observed to move with a fixed leading ray (Reese 1966). However, an orientational mechanism based on a leading ray has been discounted for both ***O. reticulatus*** and ***L. laevigata*** (Thompson and Thompson 1982). I have suggested that ***O. reticulatus*** may utilize its own chemical trail (e.g., mucus) as a directional reference (Scheibling 1981b). Alternatively, it may "set" a directional bearing at the start of a foraging period, perhaps, in relation to some environmental cue (e.g., current direction) (Scheibling 1980d).

When individuals move in the same direction, as in migratory feeding aggregations, they may be responding to environmental gradients or directional cues. For example, movements of dense fronts of ***Oreaster reticulatus*** are oriented by gradients in food abundance (see below). Castilla and Crisp (1973) demonstrated positive rheotaxis in ***Asterias rubens***. However, rheotactic orientation is unlikely in ***O. reticulatus*** since movements of individuals bear no directional relationship with prevailing currents (Scheibling 1980a, 1981b). Pabst and Vincentine (1978) suggested that directional movement of ***Astropecten jonstoni*** on sand bottoms may be oriented to wave surge or to sand ripples caused by surge. Ferlin (1973) found that large sand ripples may influence directional movements of ***Astropecten aranciacus***.

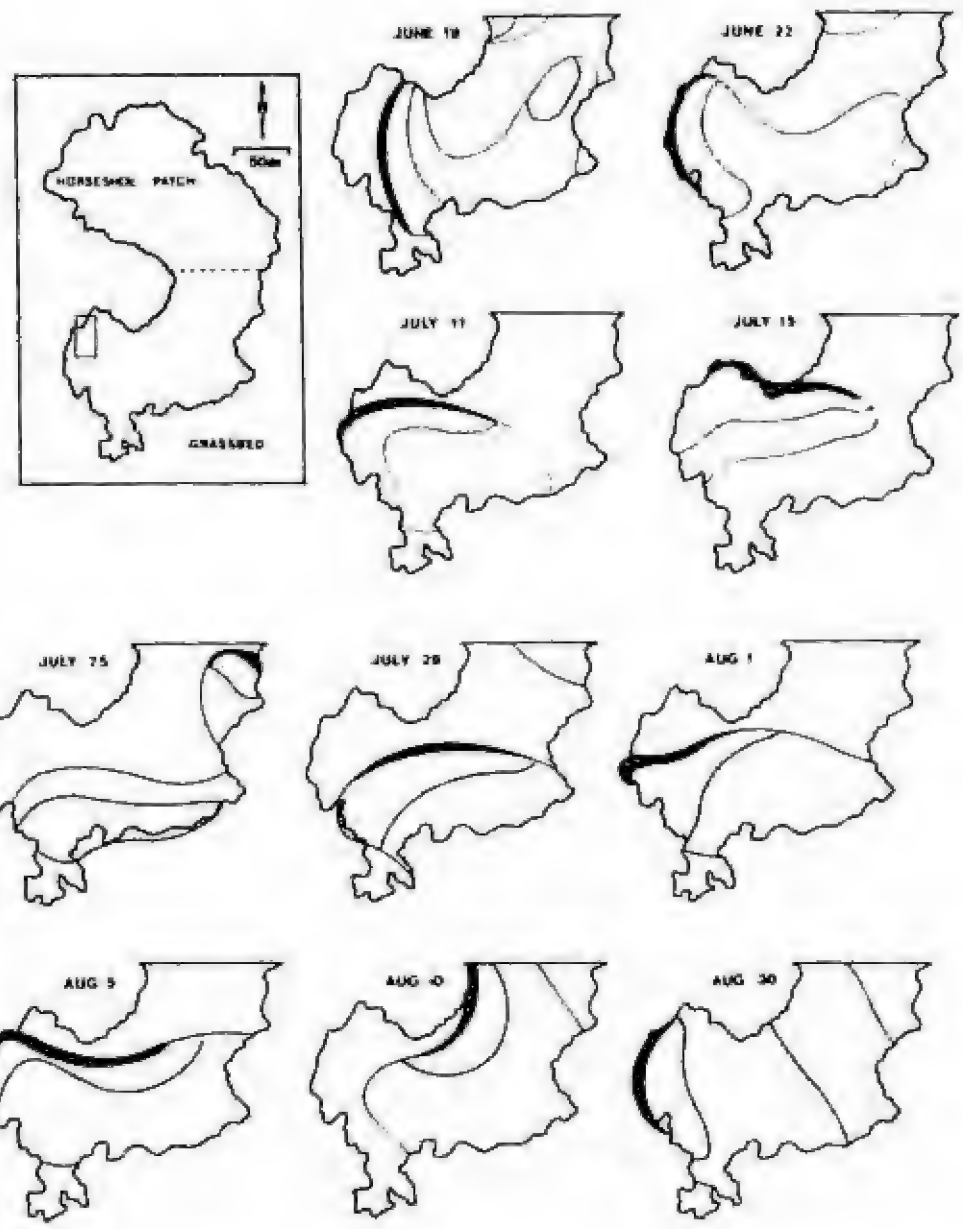

Figure 5

Map of Horseshoe Patch and time series maps of the density of *Oreaster reticulatus* in the southern arm of the patch (delineated by dashed line). Dark bands (fronts): 2−7 individuals per m^2; dense stippling: 0.2−2 individuals per m^2; sparse stippling: 0.01−0.2 individuals per m^2; blank areas: 0−0.01 individuals per m^2. Rectangle delineates study grid referred to in Figure 6 (from Scheibling 1980a).

MIGRATORY FEEDING AGGREGATIONS

In Horseshoe Patch, *Oreaster reticulatus* formed dense feeding aggregations, or fronts, that migrated throughout the sand patch (Fig 5). Average sea star density was 13 individuals per m^2 along the leading edge of the 3−5 m wide fronts, but decreased to less than 0.7 individuals per m^2 in the wake. Movements of individuals were highly directional (Fig 6). The rate of advance of fronts averaged 7 $m \cdot d^{-1}$ but varied directly with sea star density as individuals continually circumvented or straddled one another to locate suitable feeding sites. The average (± s.d.) rate of movement of individuals in a front (8 ± 2 $m \cdot d^{-1}$) was significantly less than that of individuals foraging in the wake of the front on recently grazed substrata (18 ± 7 $m \cdot d^{-1}$).

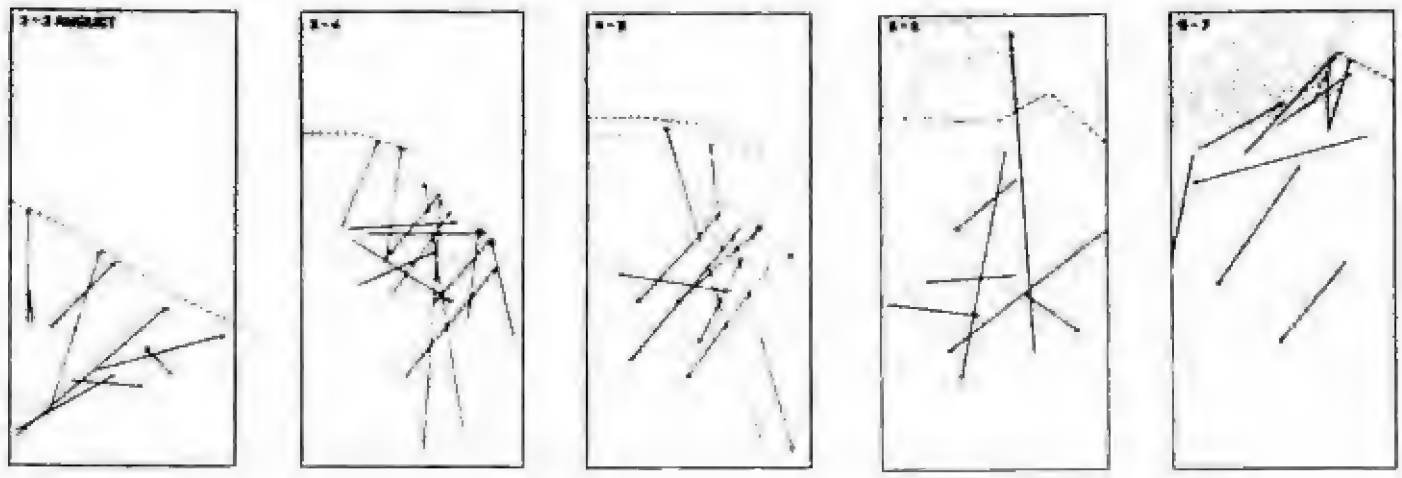

Figure 6

Daily movement vectors of *Oreaster reticulatus* within a study grid in Horseshoe Patch (See Fig 5). Shaded area represents bordering seagrass bed; dotted and dashed lines are successive positions of sea star front over 24-h periods. Note reversal in direction of movement following contact with the seagrass bed (4 August). (After Scheibling 1980a).

Sea star fronts were deflected and refracted by the seagrass bed (*Syringodium filiforme*) bordering the sand patch (Fig 5). Sea stars rarely penetrated more than a few meters into the bed; they generally moved along the border or reversed direction (Fig 6). Dense seagrass beds of this type severely restricted the mobility of *Oreaster reticulatus* and limited foraging efficiency (Scheibling 1980a,b). Aggregations of a large deposit-feeding sea urchin *Meoma ventricosa* also obstructed migrating sea star aggregations in the sand patch (Scheibling 1982b).

The formation of dense fronts of *Oreaster reticulatus* in Horseshoe Patch coincides with the peak in the annual reproductive cycle of the sea star (Scheibling 1981b). An increase in gregariousness, perhaps associated with reproductive state, may cause sea stars to form localized aggregations. This results in large-scale patchiness in the organic content of the substratum: low within grazing aggregations and high outside of them. As aggregations migrate across the patch, the movement of individuals along the leading edge is slowed as they advance into areas of high organic content. Trailing individuals, foraging upon recently grazed sediments, move greater distances. They eventually overtake those in the lead to precipitate a dense aggregation or front. A high population density and/or physical boundaries may be necessary preconditions for this phenomenon. Fronts were not observed among less dense populations of *O. reticulatus* in extensive sand bottom habitats (e.g., Buck Island Channel).

Intensive grazing by *Oreaster reticulatus* within fronts resulted in rapid turnover of surface sediments and a marked decrease in their organic content: the average chlorophyll content decreased by 64% across a front. Successive invasions of local areas of the sand patch by migratory sea star fronts occurred at 3−4 week intervals (Fig 5). This disturbance may maintain micro- and meiobenthic communities at an early successional state, and may favor species which are resistant to periodic decimation and/or opportunistic species capable of rapid colonization of "clean"

surfaces (e.g., blue-green algae).

Dare (1982) has described similar migratory feeding aggregations in a carnivorous sea star ***Asterias rubens*** on intertidal mussel beds. The sea stars moved onshore in a highly directional manner and formed dense feeding fronts which consumed all mussels in their path. Dare suggested that *A. **rubens*** may use ebb tide currents to detect and move toward the mussel populations by chemoreception or positive rheotaxis.

HOMING MOVEMENTS

Dense populations of ***Oreaster reticulatus*** may arise in isolated sand patches, such as Horseshoe Patch, due to continual recruitment from, and limited emigration to, the surrounding seagrass beds. These beds may serve as nursery areas for juvenile *O. **reticulatus***, but adults are rarely found there (Scheibling 1980b,c). To examine whether sea stars in sea grass beds are attracted to a sand patch and/or its resident sea star population, groups of *O. **reticulatus*** from Horseshoe Patch were translocated to release sites ca. 20 m into the surrounding seagrass bed and their positions were recorded after 24 h (Scheibling 1980d). The release sites were selected to vary the return direction to the patch or aggregations of sea stars within the patch.

In all experiments, translocated individuals showed significant directional movement toward the sand patch, specifically, toward the nearest aggregation of ***Oreaster reticulatus*** (Fig 7). Chemotaxis is the most likely mechanism for these movements. Sea stars translocated to sites downstream of aggregations, relative to the tidal currents, were most successful in relocating the patch within 24 h. Translocated individuals may have oriented to chemical stimuli released by feeding sea stars in the patch (e.g., mucus, digestive fluids, excretory products). Ormond, Campbell, Head, Rainbow and Saunders (1973) showed that the feeding activity of the coral-feeding sea star ***Acanthaster planci*** attracted nearby conspecifics.

The attraction of ***Oreaster reticulatus*** to sand patches containing conspecifics may result in the accumulation of large numbers of sea stars in these habitats. As density increases so does intraspecific competition for food. This may account for the small size (Scheibling 1980c), low nutrient storage capacity, and low reproductive effort (Scheibling 1981b) of *O. **reticulatus*** in Horseshoe Patch relative to less dense populations in other areas.

Similar translocation experiments have demonstrated homing behavior in the sea stars (***Astropecten jonstoni*** (Pabst and Vincineti 1978) and ***Linckia laevigata*** (Thompson and Thompson 1982). The ability of sea stars to return to favorable habitats via directional movements is clearly advantageous.

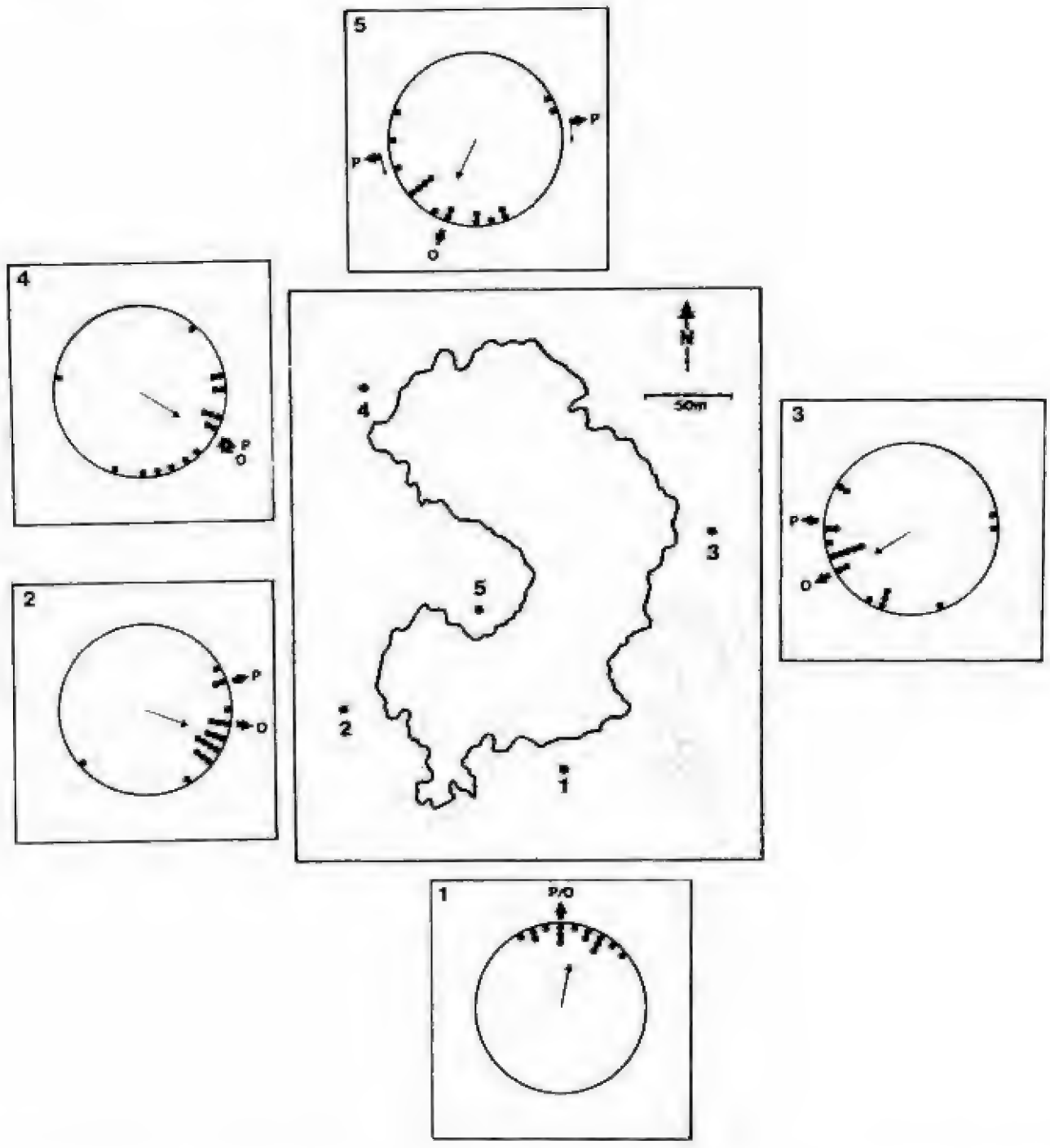

Figure 7

Movements of translocated *Oreaster reticulatus* at Horseshoe Patch. Scattergrams show directions of movement of individuals relocated after 24 h; radius vectors indicate mean directions of movement, outer arrows indicate directions to immediate area of the sand patch (P) and to the nearest aggregation of *O. reticulatus* (O) relative to each release site shown on map. (After Scheibling 1980d).

CONCLUSIONS

A pattern of directional and limited foraging movement enables *Oreaster reticulatus* to efficiently exploit microbenthic food resources on relatively homogeneous substrata. It minimizes foraging effort and the probability of re-encountering recently grazed areas, while maximizing available feeding time. The extent of movement may vary inversely with food abundance, and may result in migratory feeding aggregations or fronts under conditions of high population density and/or spatial confinement. *O. reticulatus* may home to aggregations of conspecifics via directional movement.

As radially symmetrical animals, sea stars are probably equally sensitive to their environment in all directions. Their sensory modalities, particularly chemoreception, are well known (see reviews in Reese 1966, Sloan and Campbell 1982). Further work is required to identify sensory mechanisms involved in sea star movement patterns. The ability of *Oreaster reticulatus* and other species to maintain approximately unidirectional foraging paths is particularly intriguing.

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FACTORS INFLUENCING THE LIMITS OF MIGRATORY MOVEMENTS IN TERRESTRIAL CRUSTACEANS

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ABSTRACT

The dramatic migrations performed by many terrestrial crustaceans invite comparative study by behaviorists and physiological ecologists. The potential cues for timing of migration and for orientation/navigation, and the mechanisms by which these cues are sensed and processed have not received the attention accorded vertebrate systems. Perhaps the most interesting questions about crustacean migrations concern their adaptive significance. In most cases necessity dictates that the animals migrate to the sea; they must release their larvae into high-salinity water. However, little attention has been paid to the stimuli for and limits upon movements in the other direction. The obvious hypotheses are that the animals move inland because of greater resource availability and that the distance of the movement inland is determined by their locomotor abilities and physiological tolerances. However, food availability, mobility and physical tolerances are not sufficient to account for the distributions of terresttrial crabs we have studied in the field. The limited information presently available suggests that intraspecific competition, soil characteristics (for burrowing), and availability and quality (nitrogen : carbon ratio) of food can all play important roles in determining how far inland terrestrial crustaceans migrate.

INTRODUCTION

The most dramatic migrations of terrestrial crustaceans which have marine larvae, i.e., migrations of the land-dwelling hermit crabs (Coenobitidae) and brachyuran "land crabs" (Gecarcinidae), will be the focus of this paper. These crabs are excellent research subjects; many are large, easy to observe in the field, and hardy in the laboratory. Nevertheless, in comparison with vertebrates they have received little attention from students of migratory behavior. Consequently, this paper cannot give many definitive answers about what limits their migratory movements. We will survey the available literature, pointing out basic questions that remain unanswered in the hope of stimulating further work. We will also present evidence from our work

with 3 species of terrestrial crabs which suggests that physical limitation is not the rule for these animals despite their rigorous environments. In this paper, "land crab" refers to gecarcinids, "land hermit crab" to coenobitids, and "ghost crab" to certain ocypodids. We refer to all these species by the familiar adjective "terrestrial"; under the more precise gradation of terrestriality proposed by Powers and Bliss (1983), they are "extralittoral" (land-dwelling adults, marine larvae).

The limited information that has appeared about migration of terrestrial crabs is largely descriptive and often anecdotal, ancillary to studies of distribution, ecology or physiology (Gifford 1962a, Bliss 1968, de Wilde 1973, Klaassen 1975, Henning 1975a). Very little experimental work has been done. The literature has recently been reviewed by Herrnkind (1983) and Rebach (1983), so only a brief summary will be given here.

Migration of terrestrial crabs is associated with reproductive cycles and therefore tends to be seasonal, often with a strong lunar or tidal component. This is true of both "land crabs" (Gecarcinidae) (Gifford 1962a; Klaassen 1975; Henning 1975b; Bliss, van Montfrans, van Montfrans and Boyer 1978; Wolcott and Wolcott 1982) and land hermit crabs (de Wilde 1973). Distances of migration range from tens to hundreds of meters in ghost crabs (Rao 1968, Wolcott 1978) and the red land crabs ***Gecarcinus lateralis*** (Klaassen 1975, Bliss 1979, Wolcott and Wolcott 1982) and *G. **lagostoma*** (Fimpel 1975), up to several kilometers in the blue land crab ***Cardisoma guanhumi*** (Gifford 1962a) and the land hermit crab ***Coenobita clypeatus*** (de Wilde 1973). Young ghost crabs (***Ocypode quadrata***) have been found 3 km up a fresh water stream, and *C. **clypeatus*** at elevations of 400 m on Dominica (Chace and Hobbs 1969).

Orientation relies upon several cues. During the day, ghost crabs use polarized light (Daumer, Jander and Waterman 1963); the oriented microvilli characteristic of the crustacean rhabdom confer on several species the ability to detect differences in planes of polarization of light (Goldsmith 1973). Most migratory movements occur at night; observations near artificial lights suggest that nocturnal, long-distance orientation relies on detecting the brightest sector of the horizon (Wolcott and Wolcott 1982). Near shore, extraneous light becomes less capable of diverting migrating crabs, suggesting that geotaxis and substrate vibration assume a more important role (Klaassen 1975, Bliss et al. 1978, Wolcott and Wolcott 1982), but this hypothesis has not been tested. Landmarks and prevailing winds may provide additional cues for land hermit crabs (Vannini 1975).

The spatial limitations and adaptive significance of terrestrial crab migrations are not easy to explain. The reason for the seaward leg and its terminus at the shore are obvious; larvae develop normally only in high-salinity water (Costlow and Bookhout 1968, Wolcott and Wolcott 1982). On the other hand, the adaptive value of migrating and dispersing inland, and the reasons for existing limits to those movements, are less obvious. We have used our data on the ghost crab ***Ocypode quadrata*** and the land crabs ***Gecarcinus lateralis*** and ***Cardisoma guanhumi*** to examine the traditional explanation of why and how far ranges are expanded inland.

In addressing these issues, we use the concept of "limiting factors." By this we mean a ***proximate*** cause for a given set of range limits, although we recognize that several factors would ***ultimately*** limit the range of migration. For instance, we know several reasons why crabs could not migrate to the center of the Sahara, but emphasize that we are asking what actually stops them long before they get there. For purposes of discussion, we also draw a distinction between "physical" and "biotic" interactions, while recognizing that this is a simplistic abstraction and that both types ultimately operate by physiological means.

METHODS FOR TRACKING MIGRANTS

In studying movements of crabs, we have used traditional observational techniques and newer "high-tech" methods. The physiology and behavior of terrestrial crabs are poorly suited to mark-recapture techniques. Long-term group or population studies (e.g., de Wilde 1973) are subject to error because crabs shed their exoskeletons and hermit crabs swap their snail shells. Even short-term mark-recapture has been of little use with the land crabs, which are highly mobile yet usually invisible in their burrows. Of several hundred *G. lateralis* marked with colored tape near Spittal Pond (Bermuda) in 1979, very few were seen again that season (L. Hall, personal communication). We saw two of the marked animals the subsequent year, indicating that the tape adhered satisfactorily and incidentally showing that molt interval in the field may be as long as 12 months.

Our most useful information about crab movement patterns has come from short-term observation or tracking of identified individuals. We used a night-vision scope to observe the largely nocturnal ghost crabs, but its monochrome image still left the cryptically-colored crabs almost invisible. An electronic flasher tag (Wolcott 1977) permitted line of sight tracking to several hundred meters. Addition of a radio oscillator (Wolcott 1980a) facilitated location of hidden individuals. Slightly more elaborate systems allowed transmission of data (temperature, heart rate) from free-ranging crabs (Wolcott 1980b).

Mechanical devices were more efficient than telemetry for collecting precise data on movements under some circumstances, since radio-triangulation is only approximate. The necessity of visually checking the animals' exact positions limited radio tracking to the number of individuals that could be followed simultaneously. The bare sandy surfaces on North Carolina barrier islands allowed us to track more ghost crabs with less labor, by trailing lead, split-shot fishing weights from the coxae of their major chelae on 5 cm lengths of stranded wire. The dragging weights left a record of the crabs' nocturnal movements without impeding locomotion. On the following morning, unless erased by rain or strong wind, the tracks showed where the crabs had gone and, where tracks crossed, the sequence in which they were made.

WHY DO CRABS MIGRATE INLAND?

Competition for food or suitable burrowing habitat, intraspecific aggression, and predation are the most probable selective forces for the expansion of ranges inland. Few data about these complex ecological interactions have been collected in the field. Available information indicates that inland migration serves different purposes in different species and cannot be explained by a single factor.

Competition

Competition for food could favor dispersal of terrestrial species inland from the supratidal zone, where rigorous physical conditions often lead to low biomass and low diversity. This generalization does not apply to *O. **quadrata***, because its principle food is intertidal filter-feeding invertebrates (Wolcott 1978). Fimpel (1975) and de Wilde (1973) suggest that the greatest availability of food for herbivorous crabs on Trinidade (a small island off the southern coast of Brazil) and Curaçao are inland. For the herbivorous land crab *G. **lateralis*** on Bermuda the abundance of food plants rises abruptly behind the beach. Once off the beach, however, we have observed little evidence of food depletion within the crabs' range or of large qualitative or quantitative differences in food abundance farther inland (Fig 1). Thus it is not clear that expansion of range farther inland on Bermuda would further increase food availability. There is stronger evidence that food limitation occurs in inland portions of the range of *C. **guanhumi***. Near aggregations of burrows, the ground is often denuded of vegetation (Henning 1975b, our observation, Fig 2), and manipulating the food supply affects intensity of foraging activity (Henning 1975b). This may be a secondary effect, caused by the concentration of populations in limited areas of substratum suitable for burrowing (see below).

Competition for burrows (or space suitable for burrowing) could also favor dispersal inland. There is some evidence for this in ghost crabs. Burrows are separated by minimum distances related to crab size (Hughes 1966, Lighter 1974, Fisher and Tevesz 1979), and conflict over them is common. Ghost crabs often appropriate an undersized burrow from a smaller crab instead of constructing a new one (T. Wolcott, personal observation). When rain or wind obliterate burrows on the beach, they do not quickly reappear. Ghost crabs returning from foraging in the intertidal apparently wander back into the vegetated dunes to find open holes. New burrows gradually appear on the beach over the next several days to weeks as the population shifts shoreward again (Wolcott 1978). Competition for burrows is problematic in the herbivorous land crabs. Henning (1975b) states that adult male *C. **guanhumi*** defend a burrow and at times also defend a surrounding "territory," better described as an "individual space," since the crabs change burrows frequently. The area in which burrows can reach the water table is limited. If the populations were dense enough that all burrows were occupied (apparently not always the case), then a situation analogous to that of hole-nesting birds might arise. The population would have to either cease growing numerically or disperse. Competition for burrows

Figure 1

Apparent superabundance of forage plants in habitat of *Gecarcinus lateralis*, Spittal Pond Nature Reserve, Bermuda. Burrows are found throughout the area of the photograph, from the sea (at left) well up into the hills (background, right). Individuals in the grassy areas are surrounded by an essentially ungrazed stand of a preferred food plant (St. Augustine grass *Stenotaphrum secondatum*).

probably does not cause dispersal in *G. lateralis*; rather, competition results from concentration of the adult males near the shoreline during the summer breeding season. They construct burrows there and spend much of their time fighting over them (Klaassen 1975, T. and D. Wolcott, personal observation). The function of this energy expenditure is not certain; Klaassen (1975) regards this area as a "copulation zone" where adult males congregate to court receptive females with ripe ovaries (within 5 days of ovulation). The impregnated females then remain in closed burrows nearby for about 2 weeks until the larvae are ready to hatch (Klaassen 1975). However, on Bermuda we have not seen females enter the males' "copulation burrows," have only witnessed copulations farther inland (see also Bliss et al. 1978) and have seen ovigerous females with unripe (brown) eggs migrating toward the shore from areas over 200 m inland (Wolcott and Wolcott 1982).

Intraspecific Aggression

Intraspecific aggression could disperse populations, resulting in extension of ranges further inland. We think this accounts for the presence of *O. quadrata* inland despite the lack of food there. Ghost crabs are cannibalistic (Wolcott 1978) and highly aggressive. Agonistic behavior results in spacing out of burrows, as noted above. Inland crabs are all subadults (< 2.5 carapace width, T. Wolcott, personal observation), and tracking indicates that they usually spend less than one week in the interior of North Carolina barrier islands before returning to the beach. Migration

Figure 2

Bare ground in habitat of *Cardisoma guanhumi*. Absence of understory vegetation suggests that food may be a limiting resource in these areas. Virgin Islands National Park, St. John, U.S.V.I. (Photograph courtesy Nancy M. Berdasco).

inland may allow them to escape a locally dense aggregation of adult crabs. By the time the subadults return to the shore, the adults will have dispersed or moved elsewhere. There is no evidence that juveniles of the herbivorous land crabs are similarly displaced inland (although there is evidence of cannibalism—see below), nor have we seen intraspecific aggregation in these species other than disputes over burrows.

Predation

Predation, if most intense near shore, could produce selective pressure for inland expansion of ranges. Terrestrial crabs on exposed shores are vulnerable to various avian and mammalian predators (Cott 1930; Feliciano 1960; Henning 1975b; Klaassen 1975; D. Wingate, Bermuda Department of Agriculture & Fisheries, personal communication), but there is no reason to assume that a "vulnerability gradient" extends inland beyond the point where vegetation offers appreciable cover. No data are available to test this hypothesis.

In summary, there is no single explanation for the adaptive value of inland migration by terrestrial crabs. For young ghost crabs, the value seems fairly clear. By leaving the beach they escape conspecific aggression and cannibalism, although they may also leave behind their major food sources. ***Cardisoma guanhumi*** may find increased availability of food farther from the shore, but the data are inconclusive. Existing information about *G.* ***lateralis*** does not reveal any clear advantage of

expanding the range inland. Clearly, too little is known about the basic biology of terrestrial crustaceans to generalize about the adaptive value of extending ranges inland. We need much more information about the advantages derived and the stresses avoided by such a strategy.

WHAT LIMITS HOW FAR INLAND CRABS MIGRATE?

Physiological limitation is often invoked to answer this question, with the assumption that there is a gradient of increasing cost of homeostasis or risk of death as an individual moves inland. These traditional hypotheses are relatively easy to test experimentally because they deal with physical rather than biotic factors. The two variables cited most commonly as proximal "limiting factors" for terrestrial crustaceans are water shortage and salt imbalance (e.g., Bliss 1968, Mantel and Farmer 1983, Powers and Bliss 1983). We tested their importance by measuring relevant microenvironmental variables in the field and correlating them with the animals' physiological capabilities in the laboratory. We conclude that neither water nor salt availability is likely to limit the ranges of the three species examined by us. We also reject the hypothesis that energetic cost of locomotion limits migratory movements, based on recent studies of crustacean locomotion.

Water Shortage

The ghost crab *Ocypode quadrata* is relatively permeable and has a high rate of water loss by evaporation compared to the more "terrestrial" land crabs (Bliss 1968, Herreid 1969a,b). This has been proposed as the reason it is primarily a beach crab (Bliss 1968). Ghost crabs compensate for these high water loss rates by taking up water from the sand in which they burrow (Wolcott 1976, Wolcott 1984, see also Rao 1968 for *O. cordimana*). Using tufts of 5−10 mm long setae, the crabs draw interstitial water from soil into the branchial chambers by creating a dramatic partial vacuum (to 76 mm Hg below ambient, equivalent to a 1 m column of water). This is sufficient to extract water from sand holding as little as 5% water by weight. On the North Carolina barrier islands, such sand is available within 2 m of the surface (a typical burrow depth) everywhere except under the highest dunes (Wolcott 1984). The crabs could obtain water ad libitum even in areas where they do not occur; water availability is clearly not limiting their distribution.

The red or black land crab *Gecarcinus lateralis* has also been reported to take up water from damp substrata (Bliss 1963, Bliss and Boyer 1964) by means of small (< 3 mm) setal tufts and a capillary channel to the pericardial sacs and branchial chamber (Mason 1970). We found that *G. lateralis* is less capable of extracting water from the substrate than *O. quadrata* (Wolcott 1984). The maximum suction exerted, only 30 mm Hg, corresponds to a water content of 30−40% by weight in the highly organic, water-retentive soils of Bermuda. Water in soil from burrows of *G. lateralis* never exceeded 20% and therefore was not available to the crabs (Wolcott 1984). The crabs must rely on preformed water in food and upon free water (rain, dew). When

water is not available, the crabs remain in their burrows where the water-saturated air minimizes evaporative loss. Availability of water shows no gradient from shore to interior of the island and consequently cannot explain the restriction of *G. lateralis* to within 250 m of the shore.

The blue or white land crab *Cardisoma guanhumi* lives up to 5 km inland along the banks of canals in south Florida (Gifford 1962a, Herreid and Gifford 1963) and streams in Brazil (Fimpel 1975), where sharp gradients in water availability would not be expected. However, this species is limited to areas where it can dig down to the water table and maintain a pool at the bottom of the burrow (Herreid and Gifford 1963), i.e., to areas where water lies within about 2 m of the surface (Feliciano 1960, Herreid and Gifford 1963). It is not clear from these reports whether suitable low-lying habitat is available farther inland than 5 km. If it is, then water availability cannot be limiting inland penetration along canals and streams, although it clearly does determine the small-scale distribution of burrows in the *C. guanhumi* colonies we have visited on Bermuda, Bimini and southern Florida (T. and D. Wolcott, personal observation).

Salt Balance

Salt relations of terrestrial crustaceans have commonly been viewed in light of presumed water shortages. Continued intake of salts in food and inadequate water for excretion lead to salt loading. On the other hand, if sufficient water were available but were markedly hyposmotic to the crabs' hemolymph, salt shortage could become a problem. The latter appears to describe the situation of the three species we have examined. All of the water sources available inland are dilute. Ghost crabs burrowing farther than 20 m from the surf on the North Carolina barrier islands encounter the fresh water lens (< 1 $^{o}/oo$ that overlies the salt water in the interstices of the sand. *Gecarcinus lateralis* relies on rain and dew (Wolcott 1984). *Cardisoma guanhumi* uses the pool in its burrow, which is fresh water except in intertidal areas (Herreid and Gifford 1963). We therefore tested the hypothesis that salt shortage limits the ranges of the two species to which we had access (*O. quadrata* and *G. lateralis*). The data indicate that it does not; both species are capable of osmoregulating under conditions simulating those beyond the normal range limit. The information available suggests that salt is not limiting for *C. guanhumi* either.

Ghost crabs are excellent ion conservers. They osmoregulate over a fairly wide range of salinities under traditional immersion regimes (Flemister and Flemister 1951, Flemister 1958, Gifford 1962b), but under ecologically realistic conditions (sand dampened with the test salinities), they are able to regulate down to fresh (< 1 $^{o}/oo$) water (Hall 1982). Two major mechanisms available only in terrestrial habitats contribute to this ability.

Unlike aquatic crabs, terrestrial species can limit their contact with, and select among, available osmotic environments. For instance, *Coenobita clypeatus* can proportion its "drinking" from a variety of available salinities according to its osmotic requirements (de Wilde 1973). If only very dilute water is available, terrestrial crabs

may restrict intake to what is needed to replace evaporative losses and excrete wastes. They are not subject to salt gain or loss through the general body surface, since they are surrounded by air rather than water. In short, they are able to become essentially closed systems under adverse osmotic circumstances rather than having to expend energy to maintain homeostasis in an open system.

The second mechanism available to terrestrial crabs is extrarenal reprocessing of urine. Whereas urine of aquatic crabs is dispersed into the water as soon as it leaves the nephropore, that of terrestrial crabs is at least theoretically available for further handling. This is particularly important because the antennal gland, the "kidney" of crabs, is only capable of producing isosmotic urine and is therefore ineffective as an organ of osmoregulation (Mantel and Farmer 1983). The gills, which can produce strong osmotic gradients and are the major osmoregulatory organs of aquatic crabs, cannot pump ions to or from an aerial medium. Terrestrial crabs could transfer isosmotic urine from the nephropores to the branchial chambers, pump part of the salts from the urine back into the blood, and then discard a final waste product hyposmotic to the blood.

The morphology of terrestrial crabs is consistent with such a mechanism. The nephropores, particularly of the more terrestrial species, are located such that urine would tend to trickle toward the Milne-Edwards openings at the front of the branchial chambers. In the Gecarcinids the pores are actually behind the third maxillipeds and could eject urine away from the body only if the mouthparts were substantially displaced.

Production of hyposmotic waste has been demonstrated in our laboratory. When ghost crabs are held in funnel-bottom containers over oil traps and infused with isosmotic physiological saline (after Skinner, Marsh and Cook 1965), the discarded fluid is osmotically and ionically similar to blood and urine. When the crabs are infused with distilled water, the waste fluid becomes markedly hyposmotic to blood, largely because of a marked decline in its sodium and chloride content (Fig 3; data from Wolcott and Wolcott, in press). We are currently examining whether this occurs by extra-renal resorption of salts (as we expect) or by extra-renal secretion of water, and what organs are involved in the process.

Together these abilities allow ghost crabs to survive under simulated natural burrow conditions, even on acid-washed quartz sand dampened with deionized water, for weeks (Hall 1982). They could survive the osmotic conditions anywhere on the barrier islands for many times longer than they remain inland. Thus salt availability cannot account for their distribution.

Gecarcinus lateralis possesses similar mechanisms, and it too is able to regulate blood concentrations under conditions of extreme ion deprivation. Like ghost crabs, ***G. lateralis*** produces a dilute excretory product when subjected to dilution stress (Wolcott and Wolcott, unpublished data). When held under ecologically relevant conditions (in a dry cage with access to a dish of distilled water) it is able to osmoregulate indefinitely using the salts in its food (Mantel, Bliss, Sheehan and Martinez 1975). Even if salt-free albumin "flavored" filter paper is the sole "food" passing through the gut, these crabs show only minor decreases in blood osmotic and

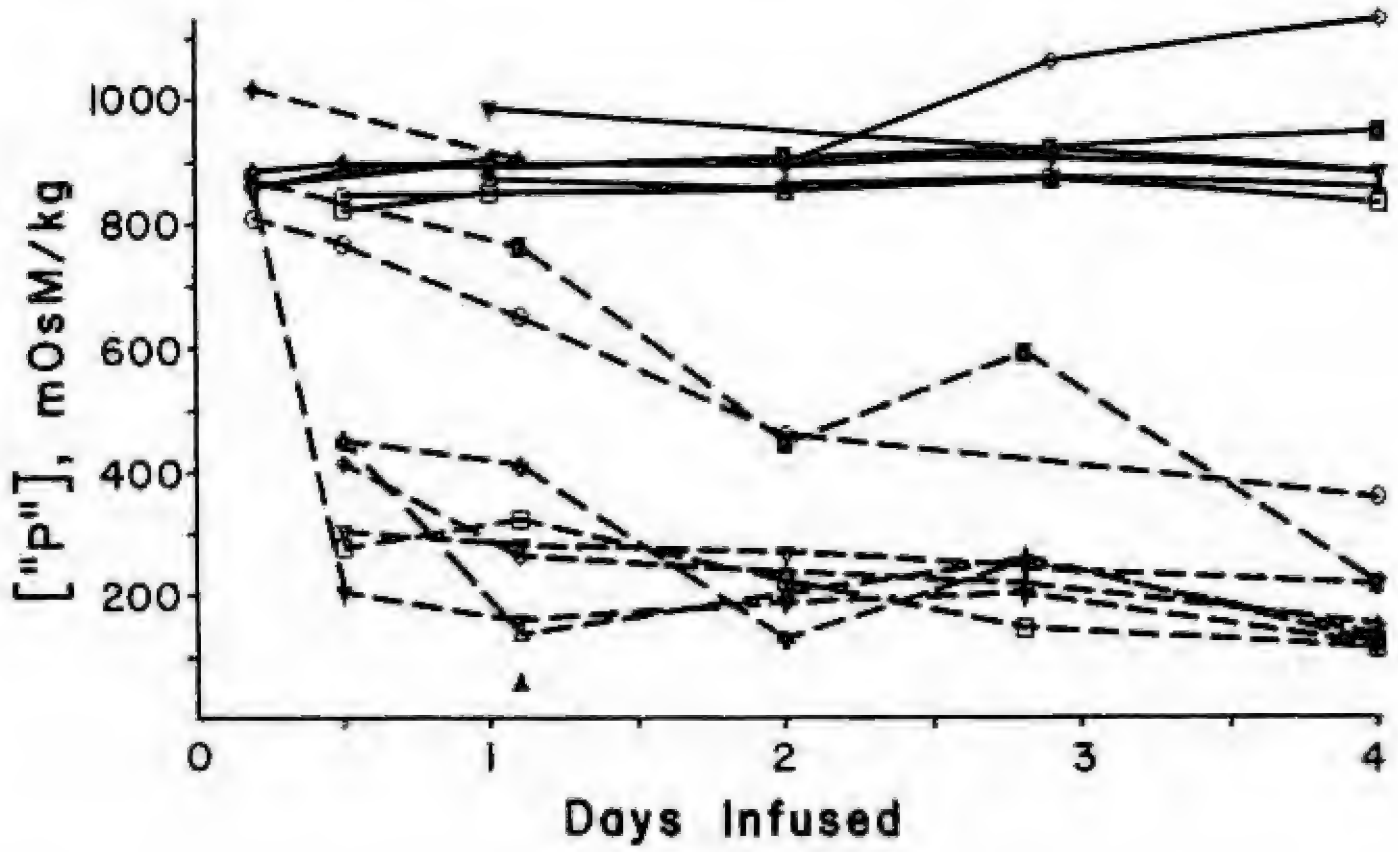

Figure 3

Salt conservation by extrarenal modification of urine (originally isosmotic to blood) in *Ocypode quadrata*. Solid lines: crabs that have been infused with isosmotic saline (volume loaded) release a final excretory "product" ("P") isosmotic to blood and urine (800–900 m $OsM \cdot kg^{-1}$). Dashed lines: crabs infused with deionized water (volume loaded + dilution stress) release "P" markedly hyposmotic to blood and urine.

ionic concentrations over six weeks (D. Wolcott, unpublished data). Strict ion conservation and utilization of dilute water sources may be characteristic of the genus; *Gecarcinus lagostoma* chooses fresh water exclusively over seawater (Fimpel 1975) in the laboratory.

The existence of highly effective ion conservation mechanisms suggests that salt availability is unlikely to limit the range of *G. lateralis* in nature. This conclusion is supported by the lack of a gradient in salt content of food plants along transects from the shore to well inland of the crabs' range limit (Fig 4, from T. Wolcott, in preparation), even when accumulation of salt spray on leaf surfaces was considered. A variable that shows no gradient cannot present a limit. Salt availability in plants inland of the crabs' normal range was tested with land crabs depleted of salts by forced partial immersion in fresh water. One group was then fed the ion-free "flavored" filter paper, while a second received inland vegetation. Blood electrolytes declined further in the filter paper group but returned toward initial values in the vegetation group (T. Wolcott, unpublished data). These values, determined from the conductivity of ashed blood samples (in the absence of more elaborate instrumentation), are indicative of total inorganic salts. They suggest that salt content of inland vegetation is sufficient for maintaining electrolytic balance, although we cannot exclude the possibility that some particular ion (e.g., Na^+) is limiting.

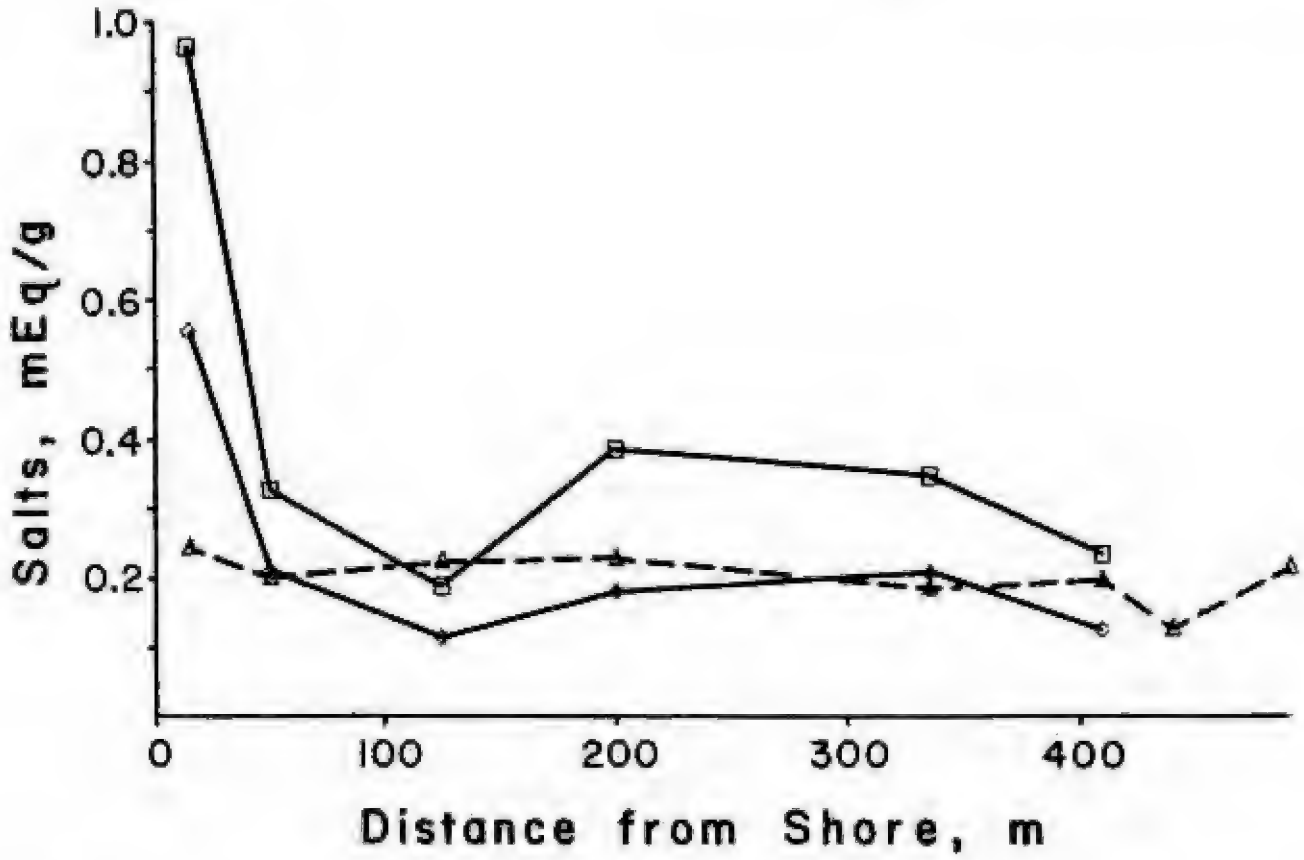

Figure 4

Salt availability (including surface deposits from spray) in preferred food plants of *Gecarcinus lateralis* near Spittal Pond, Bermuda, as a function of distance from shore. There is no significant gradient in salt content of plants (except in a narrow zone affected by spray) from near shore to the limit of the crabs' range (about 200 m inland), to high hillsides well beyond the range limit. Solid lines: Australian (whistling) "pine" (*Casuarina equisetifolia*); dry weight basis (squares) and wet weight basis (diamonds). Salts available to the crabs lie between these extremes since fallen "leaves" of this plant are consumed partly dry. Dashed line: St Augustine grass (*Stenotaphrum secondatum*), wet weight basis. This grass is normally consumed green. (Total salts estimated by conductivity of resuspended ashed samples of plants.)

The information available for *Cardisoma guanhumi* indicates that salt availability is not limiting the range of this species either. The adults are capable of osmoregulating down to fresh water (Herreid and Gifford 1963) probably by mechanisms similar to those of *O. quadrata* and *G. lateralis*. The salt content of water at the bottom of the burrows drops from brackish to fresh within a few meters of the shore (Herreid and Gifford 1963), but the crabs range extends inland far beyond the end of the salt-availability gradient. On the other hand, Fimpel (1975) states that *C. guanhumi* is found in Brazil only where brackish water is available.

Energetics of Locomotion

The energetic cost of locomotion is presumably proportional to the distance to be traveled and can be further elevated by behaviors which reduce risk to adults or larvae. For instance, ovigerous females leave the most direct seaward route to detour around pools of standing water, thus preventing premature hatching and mortality of larvae (de Wilde 1973, Wolcott and Wolcott 1982). Nevertheless, the first impression is that crabs move long distances with ease. Land hermit crabs are capable of moving 500 m or more in a night (de Wilde 1973) although time spent in finding food and water can reduce the average speed to 100 m per night or less. Land crabs typically

walk at > 2.5 $cm \cdot s^{-1}$ which, if sustained, would carry them upwards of 100 m per hour. Ghost crabs, which are capable of sprinting at several $m \cdot s^{-1}$, are capable of sustained aerobic walking at 200 $m \cdot hr^{-1}$ (Full and Herreid 1983) and we have tracked them over 700 m in a night. C.F Herreid and his associates at SUNY-Buffalo have done extensive work in the energetics of crab locomotion and have demonstrated that the cost of walking a kilometer or more would be a minor component of total respiration (Herreid 1982). It appears then, that these crabs could afford both the time and the energy to migrate kilometers, yet most populations are limited to within a few hundred meters of the shore. Radio tracking of migrating crabs to determine the average speed and duration of locomotion would shed additional light on locomotor costs.

DIRECTIONS FOR FUTURE RESEARCH

If the interactions of physiological tolerances with the physical environment do not account for the inland range limits of these terrestrial crabs, we need to examine interactions with other components of the biological community. Food is a universally required resource, and we might hypothesize that it becomes limiting with increasing distance from shore. This is probably true for ghost crabs, which rely on beach macroinvertebrates for 90% of their diet (Wolcott 1978). It seems absurd for Bermudian *G. lateralis*, which have superabundant food within and beyond the normal range (Fig 1).

Many herbivores, like *G. lateralis* , appear to live in the midst of plenty. Why don't they expand their ranges? Why aren't their populations larger? It is becoming clear from a number of studies that food quality (content of some specific nutrient, usually nitrogen) can limit herbivores even when food is abundant and that this has profound ecological implications.

The herbivorous land crabs and land hermit crabs behave as though nitrogen is a limiting nutrient. Carrion and other high-protein foods are preferred foods of the coenobitids, as are fresh feces of larger animals (Grubb 1971, de Wilde 1973). Gecarcinids avidly take high-nitrogen foods, including carrion and live prey, whenever available (Herreid 1963, Ehrhardt and Niaussat 1970, Fimpel 1975, Henning 1975a, Bliss et al. 1978). One of our students (N. Berdasco) found that on St. John, U.S. Virgin Islands, *C. guanhumi* consistently selects meat over normal forage plants in field trials. Caged *G. lateralis* in our laboratory become markedly more aggressive toward moving objects shortly after molting (T. and D. Wolcott, personal observation), when protein requirements are presumably elevated by the synthesis of new tissue to fill out the new shell. Food quality appears to limit tissue growth and nitrogen intake in *G. lateralis* (Wolcott and Wolcott 1984), because the crabs are unable to process a sufficient volume of the normal low-nitrogen diet to achieve optimal nitrogen intake.

Food quality also modulates cannibalistic behavior in *G. **lateralis***. Crabs fed the normal low-nitrogen diet ad libitum quickly catch and consume conspecific juveniles placed with them in a vegetation-filled bucket, whereas adults fed the same diet supplemented with soybeans are much less cannibalistic and aggressive (Wolcott and Wolcott 1984). Cannibalism also appears to occur in *G. **planatus*** (Ehrhardt and Niaussat 1970) and *G. **lagostoma*** (Fimpel 1975). Land hermit crabs (***Coenobita clypeatus***) are also cannibalistic in the laboratory (de Wilde 1973) if they are not given "the right kind of treatment."

Cannibalism is potentially an efficient feedback mechanism for population regulation because it acts at the level of recruitment instead of reproductive output. A species with a pelagic larva should keep reproductive output high even if local conditions are poor, because of the uncertainty of both larval survival and conditions juveniles will encounter wherever they metamorphose and settle. Such a species, by modulating cannibalism, could produce a response more appropriate to local conditions. Locally low food quality (nitrogen availability) would lead to increased cannibalism, which would both lower recruitment and channel available nitrogen (some of it derived from plankton, a source otherwise unavailable to adult crabs) into the breeding members of the population. Anecdotal information suggests this does occur. Dr. David Wingate of the Bermuda Department of Agriculture and Fisheries, in the course of re-establishing native plants in the Nonsuch Island Preserve, scattered castor-bean pomace as a high-nitrogen organic fertilizer. The net result was an outbreak of *G. **lateralis*** and substantial depredations upon his plantings. This local outbreak was almost certainly attributable to locally increased recruitment, rather than to greater output of larvae into the currents surrounding the isolated island.

What relationship has food quality to the bounds of migratory movements of herbivorous terrestrial crustacians? If cannibalism of juveniles is a vital nitrogen input when availability of nitrogen to adult crabs is low, then during periods of poor food quality it would be advantageous for adults to remain near shore and to harvest recently settled juveniles. The result would be a contracted range and low recruitment. At times of good food quality, cannibalism would decrease in importance as a source of nitrogen, successful recruitment would lead to a growing population, and the advantages of concentrating near the shore would diminish, allowing the population to disperse inland. The mechanisms are demonstrable in the laboratory and the processes seem logical. Now we must turn to field experiments to rigorously test the hypothesis.

CONCLUSIONS

We have attempted to determine what sets the bounds for migratory patterns in crabs, basically marine animals that have invaded the physically variable and potentially stressful terrestrial habitat. Despite the expectation that the limiting factors would be "physically dominated" ones (Sanders 1968), we find that physiological limitation is not the rule. In fact, none of the simple answers seems adequate. To even ask the right questions, we need a more thorough understanding of field biology than presently exists for most terrestrial crustaceans.

ACKNOWLEDGMENTS

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CHAPTER THREE

FISH MIGRATIONS

The migrations of fishes are extensive and well documented, and the mechanisms which ***might*** guide their direction and timing have been intensively studied both in the laboratory and in the field. These subjects are well reviewed in Harden-Jones (1968); Leggett (1977); Northcote (1978) and McCleave, Arnold, Dodson and Neill (1984).

With a few notable exceptions, students of fish migration have, until relatively recently, been primarily concerned with descriptions (path, timing, duration, speed, precision) and with the identification of orientation cues and their mode of detection (olfactory, celestial, electromagnetic, inertial, etc.). While generalizations are dangerous, I would also assert that undue emphasis has been placed on studies of spectacular, large-scale migration; on the concept of precision as it relates both to timing and orientation; and on the ethological as opposed to the ecological and evolutionary aspects of migration. The field has suffered as a result. A more detailed treatment of this question is given in Leggett (1984).

Relatively recently, students of fish migration have begun to broaden their view and to challenge old ideas. An invigorating new wave of critical, creative thought has engulfed the field and major conceptual and analytical advances are resulting (see McCleave et al. 1984).

Two areas where significant new insights are evolving concern the relationship between physical features of the environment and migrations, and the adaptive significance of migrations (in both an ecological and an evolutionary sense). The symposium contributions reported in this chapter were selected to illustrate these new developments and to highlight the advantages that can accrue from viewing migrations, whether of fish or other organisms, from a broader perspective.

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THE ROLE OF MIGRATIONS IN THE LIFE HISTORY EVOLUTION OF FISH

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ABSTRACT

The thesis is advanced that the life history evolution of fish is significantly influenced by macro- and microscale migrations. In particular it is argued that migrations can, when strongly coupled with reliable environmental signals, greatly reduce the impact of environmental variance on reproductive success. This behavioral dampening of variability in reproductive success can significantly alter the intensity of selection for adaptations at the life history level. Failure to accurately identify that portion of the total environmental variability which is actually experienced by fishes can lead to the incorrect conclusion that observed life history traits are inconsistent with the predictions of theory. These ideas are illustrated by reference to the macroscale reproductive migrations of adult American shad (*Alosa sapidissima*) which spawn in rivers along the Atlantic coast of North America and to the microscale migrations of the larvae of the beach-spawning capelin (*Mallotus villosus*).

INTRODUCTION

In his 1954 paper "The Population Consequences of Life History Phenomena" Lamont Cole asked the deceptively simple question, "Why do animals reproduce more than once?" His analysis of this question led him to conclude that, "The reproductive potentials of existing species are related to their requirements for survival; that any life history features affecting reproductive potential are subject to natural selection; and that such features observed in existing species should be considered adaptations just as purely morphological or behavioral patterns are commonly so considered." This observation was not new (see Fisher 1930, Severtsov 1941), but the apparent paradox of repeat reproduction identified by Cole drew new attention to the concept of life histories as reproductive strategies shaped by natural selection. The result was the rapid development of a new theory related to the evolution and adaptive significance of life history patterns in animals and plants. This theory has been extensively reviewed in Stearns (1976, 1977).

In essence, life history theory argues that patterns in life history or reproductive characters (the two terms being largely synonymous) represent population-specific adaptations to environmental variability that influence reproductive success. More specifically, for fishes and other organisms in which reproductive success is determined primarily by mortality in the early developmental stages (see Cushing 1975, Dragesund and Nakken 1973, Leggett 1977), life history theory argues that the particular combination of life history traits exhibited by a population is a function of the predictability of the reproductive environment: in highly predictable environments, early maturity, high fecundity and suicidal reproduction (semelparity) should predominate; in stochastic environments, delayed maturity, reduced fecundity and repeated reproduction (iteroparity) are expected (Stearns 1976). The arguments underlying this theory are as follows: in predictable environments, reproductive success is largely constant in time, while the probability of surviving to reproductive age declines with increasing time to maturity. Individuals should therefore reproduce at the youngest age possible and allocate the maximum amount of energy possible to that reproduction (the so-called energy allocation hypothesis, Cody 1966). Somatic growth is thus sacrificed and post-reproductive mortality is high. In stochastic environments the probability of reproductive failure in any given year is higher. Under these conditions, fitness is improved by spreading the reproductive effort over several years thereby avoiding a single catastrophic reproduction. This demands that in iteroparous populations some of the energy allocated to reproductive products in semelparous populations be diverted to growth and survival.

Stearns (1977, 1980) has seriously questioned the extent to which the available data on life history adaptation support the theory. In his 1980 paper in particular, he questions the very existence of life history strategies at the intraspecific level. Stearn's papers clearly document the fact that life history parameters are not always consistent with the predictions of theory, and that physiological problems, at least, can "overwhelm the expected co-adaptations of life history traits." In my opinion, these inconsistencies are not sufficient to justify the abandonment of life history theory. They do indicate, however, that our approach to the study of life history adaptations has been naive. In the development of life history theory, too little attention has been paid not only to physiology, but also to behavioral adaptations. In addition, in tests of the theory, the correlation between measures of environmental variability and reproductive success has too often been assumed rather than measured.

In fishes in particular, migratory behavior and reproductive requirements are frequently tightly linked, often in spectacular ways, and are often further moderated by physiological adaptations. The reproductive migrations, the strong home stream fidelity, and the extensive migration-related changes in physiology exhibited by salmon provide dramatic examples.

Dealing specifically with the link between migratory behavior and life history tactics, it is important to note that migrations which are tightly coupled to reliable environmental signals may operate to greatly reduce the environmental variance actually experienced by the adults, their offspring, or both. Hence environments that at first glance appear totally unpredictable with respect to parameters known to be

important to reproductive success can, through appropriate behavioral responses, be rendered highly predictable. The extent to which life history traits conform to the predictions of theory should therefore be a function, not of the apparent variance in the environment, but of the variance actually experienced by the individual. This will depend on the nature of the environmental variance and the extent to which behavioral and other adaptations are successful in damping its frequency and amplitude.

In this paper I investigate this idea by examining the interaction between behavioral and life history adaptations to environmental uncertainty in two fish species, the anadromous American shad (*Alosa sapidissima*) and the beach-spawning capelin (*Mallotus villosus*). In choosing these species I seek to demonstrate the potential importance of both macro- and microscale migrations as moderators of environmental uncertainty, and to illustrate the ways in which such behavior can influence the existence and form of life history adaptations.

Macroscale Migrations: Reproductive Migrations in American Shad

American shad spawn in the spring in most major rivers along the Atlantic coast of North America from Florida to New Brunswick (Leggett and Carscadden 1978). Juvenile shad migrate to sea in the fall of their first year (Walburg and Nichols 1967). Shad migrate extensively at sea and fishes from all Atlantic coast populations follow a common route and are exposed to similar environmental and feeding conditions (Leggett and Whitney 1972, Neaves and Dupres 1979). Adult shad home to their natal rivers to spawn with considerable precision (Carscadden and Leggett 1975a, Leggett 1976). Individual populations can be identified on the basis of meristic and morphometric traits and are believed to be genetically distinct (Carscadden and Leggett 1975a,b; Gabriel, Leggett, Carscadden and Glebe 1976; Shoubridge 1978).

Reproductive success in American shad is strongly linked to the thermal characteristics of the home river during the spawning and immediate post-spawning period. Figure 1, developed from bioassay data in Bradford, Miller and Buss (1968), illustrates the relationship between water temperatures and the proportion of eggs surviving to the early larval stage. Maximum survival occurs at temperatures between 15−21°C. At higher and lower temperatures survival declines dramatically. Leggett (1976) also demonstrated the dependence of year class strength in shad on water temperatures in the spawning and immediate post-spawning period.

The initiation of freshwater spawning migrations in individual populations of American shad is tightly coupled to specific water temperatures. The peak of river entry in all Atlantic coast rivers occurs at approximately 15°C, and the duration of the river entry is directly proportional to the duration of optimal spawning temperatures (Fig 2). This precise timing serves to maximize the probability that adults will arrive on the spawning grounds when temperature conditions are optimal for egg and larval development, while at the same time it minimizes the time adults must spend in freshwater. Since adults do not feed in freshwater (Leggett 1972), and the energy costs of the freshwater migration are high (Glebe and Leggett 1981a,b), this timing also reduces the drain on somatic energy reserves and increases the probability of adult

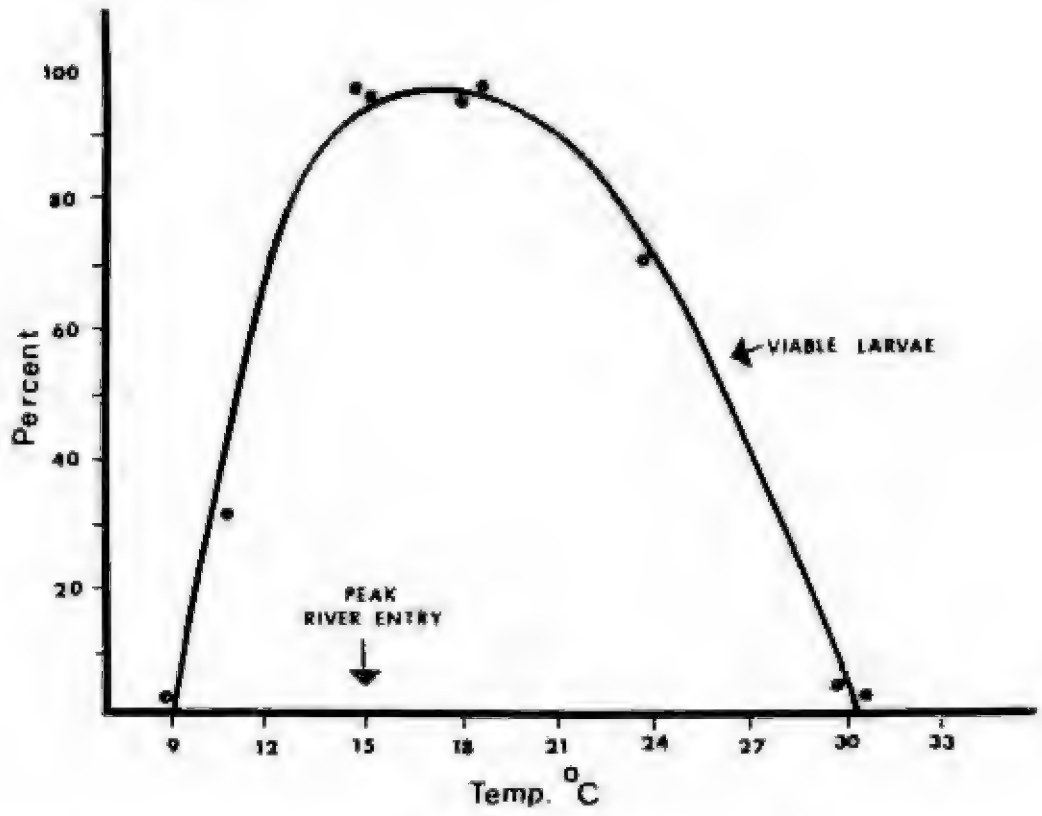


Figure 1

Relationship between water temperature and percentage of American shad eggs producing viable larvae as determined by bioassay. Average temperature at the time of river entry by migrating adults is also shown.

survival.

Upriver migration rates subsequent to river entry are insensitive to changes in water temperature (Leggett 1976). The precision of the coupling of spawning activity with optimum temperature conditions thus depends both on the timing of river entry with respect to temperature *and* the rate of change in temperature subsequent to that time. It is evident from Figure 2 that this rate varies significantly with latitude. The generality of this observation was demonstrated by Shoubridge (1978). However, given the strong homing behavior of shad and the resulting reproductive isolation of populations, such river-specific differences could be accommodated by population-specific differences in migration rate which are tuned to local rates of warming.

A more critical parameter, in terms of spawning success, is the year-to-year variance in the thermal regime within rivers. Two discrete types of thermal variance are possible: in Type A the time of occurrence of a specific temperature varies between years, but the rate of warming is constant; in Type B the time of occurrence of a specific temperature is constant, but the rate of warming is variable. These two forms are illustrated in Figure 3. It is known that shad behaviorally accommodate Type A variance by adjusting the timing of river entry in response to year to year variation in the time of occurrence of specific temperatures (Leggett and Whitney 1972, Leggett 1976). However, because shad do not adjust rates of upriver migration in response to temperature (possibly because of the significant added migratory energy costs that this would entail; see Glebe and Leggett 1981a,b), the effectiveness of the coupling of spawning and temperature conditions optimal for egg and larval development should be negatively related to the variance in the rate of warming relative to the mean rate (Type B).

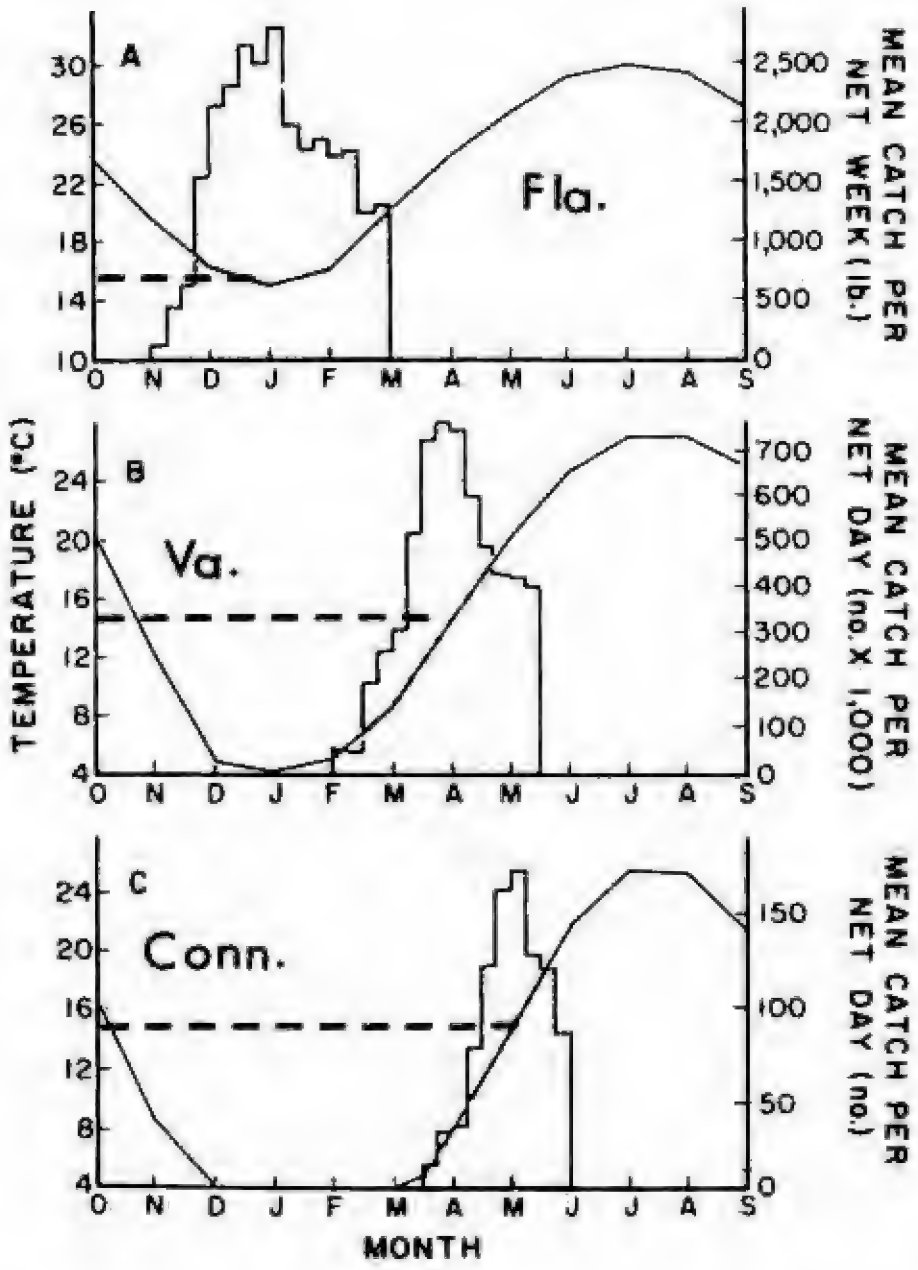


Figure 2

Relationship between mean monthly water temperatures and the timing of river entry by mature shad in three Atlantic coast rivers. A: Florida; B: Virginia; C: Connecticut. Temperature at the time of the peak river entry is indicated by the horizontal dashed line. (Redrawn from Leggett and Whitney 1972.)

Of course, the two types of variance are unlikely to operate independently. Of greater importance is the question: is there a systematic change in the relative importance of the two forms of thermal regimes over the species range? To address this question I characterized Type A and Type B variance by plotting the relationship between slope and intercept of the time/temperature relationship. In the extreme form, Type A variance yields a vertical line; Type B a horizontal line (Fig 3). In reality, because of the interaction of Types A and B, the relationship between slope and intercept is likely to fall intermediate between the extremes (Fig 4A). To determine the relative importance of Type A and Type B variance in the thermal regimes of Atlantic coast rivers Shoubridge (1978) examined the relationship between the slope and intercepts of time temperature relations for several Atlantic coast rivers for which long-term temperature records were available. The results indicate a systematic increase in Type B variance as the latitude of the home river increases. This change is illustrated in Figure 4B which presents data for four rivers which extend over a

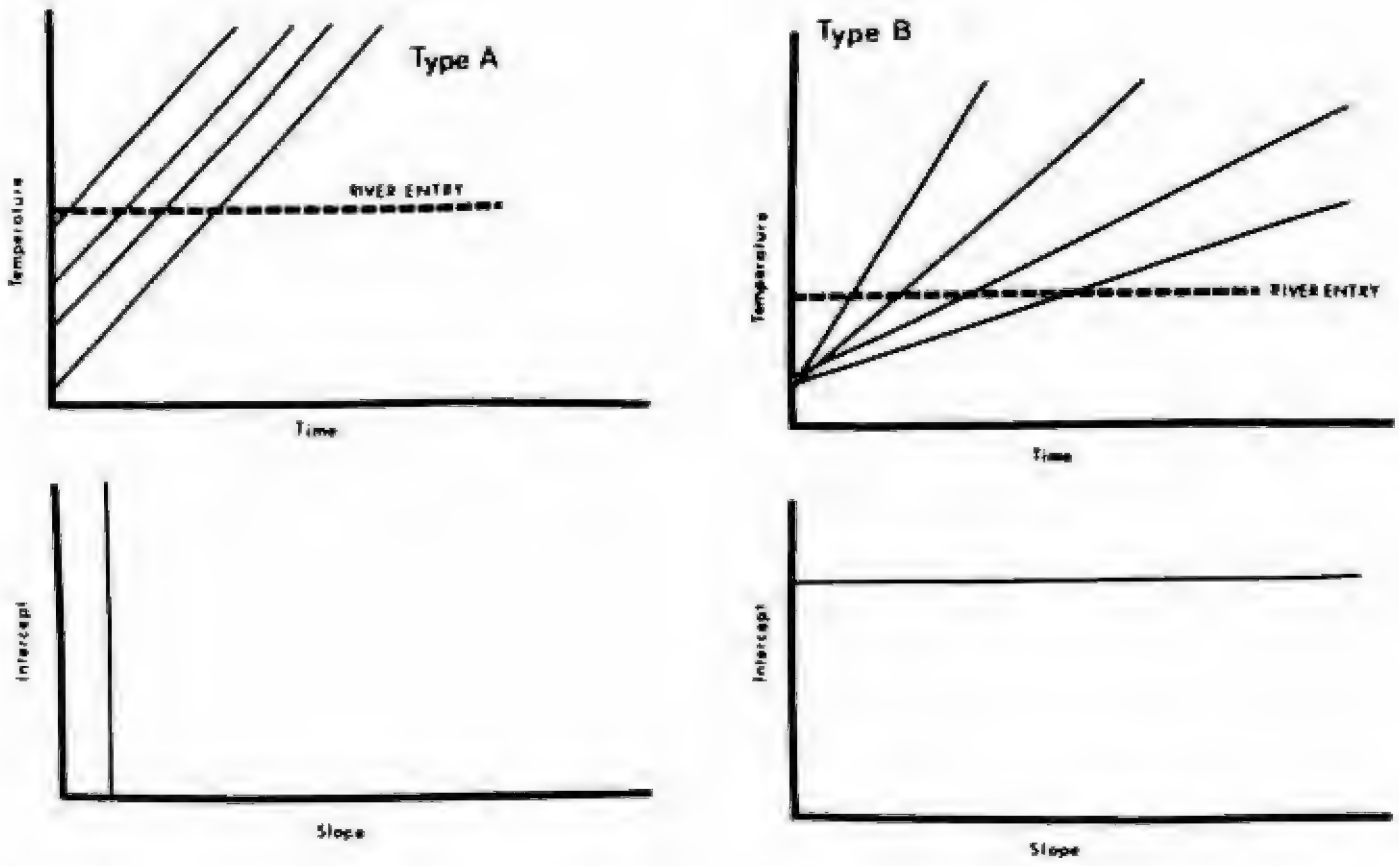


Figure 3

Contrasting forms of thermal variance (upper panel) and their representation as a plot of intercept vs. slope (lower panel).

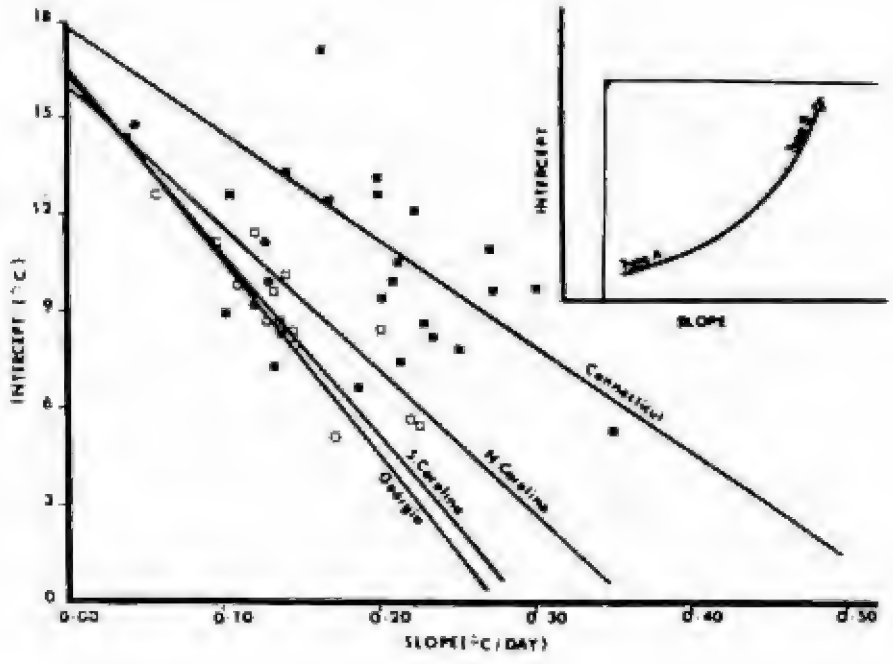


Figure 4

Hypothetical (insert) and actual relationships between the slope and intercept of the thermal regimes in Atlantic coast shad rivers.

significant portion of the species' Atlantic coast range. The reduction in the duration of the optimal thermal window for reproduction (Fig 2), together with the increase in biologically relevant variance with latitude, reduces the efficacy of adjustments in the timing of river entry as a means of compensating for variance in the thermal regime. Year-to-year variability in reproduction should, therefore, increase with latitude.

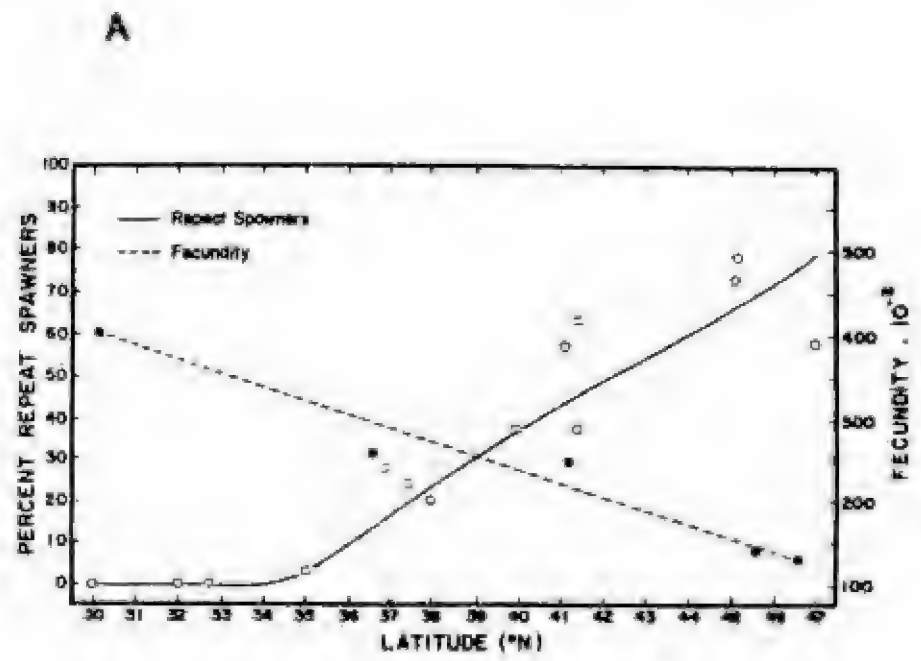


Figure 5

Changes in the frequency of repeat reproduction and fecundity (A) and in the pattern of energy allocation to gonads vs. post reproductive reserves (B) of Atlantic coast American shad populations as uncertainty of the reproductive environment increases with latitude. (Redrawn from Leggett and Carscadden 1978 and Glebe and Leggett 1981b.)

Life history theory predicts that under these conditions the following changes in life history traits should accompany increasing latitude: (a) the frequency of repeat reproduction should increase; (b) the number of eggs produced per female per reproductive period should decrease; (c) energy allocation to migration should increase at the expense of reproductive products; and (d) age at maturity should increase. All four predictions are met (Fig 5, Table 1).

Table 1

Mean (SD) age at maturity of shad from five Atlantic coast populations. Populations having similar mean ages at maturity are indicated by the same letter in the significance column (Duncan Multiple Range; Student-Neuman-Keuls $p < 0.05$).

Males			Females		
Mean Age at Maturity	Significance	River System	Mean Age at Maturity	Significance	River System
3.8	a	St. Johns (Fla.)	4.2	a	St. Johns (Fla.)
4.1	b	Connecticut	4.5	b	St. John (N.B.)
4.2	b	York	4.6	b	Miramichi
4.2	b	St. John (N.B.)	4.7	c	York
4.2	b	Miramichi	4.8	c	Connecticut

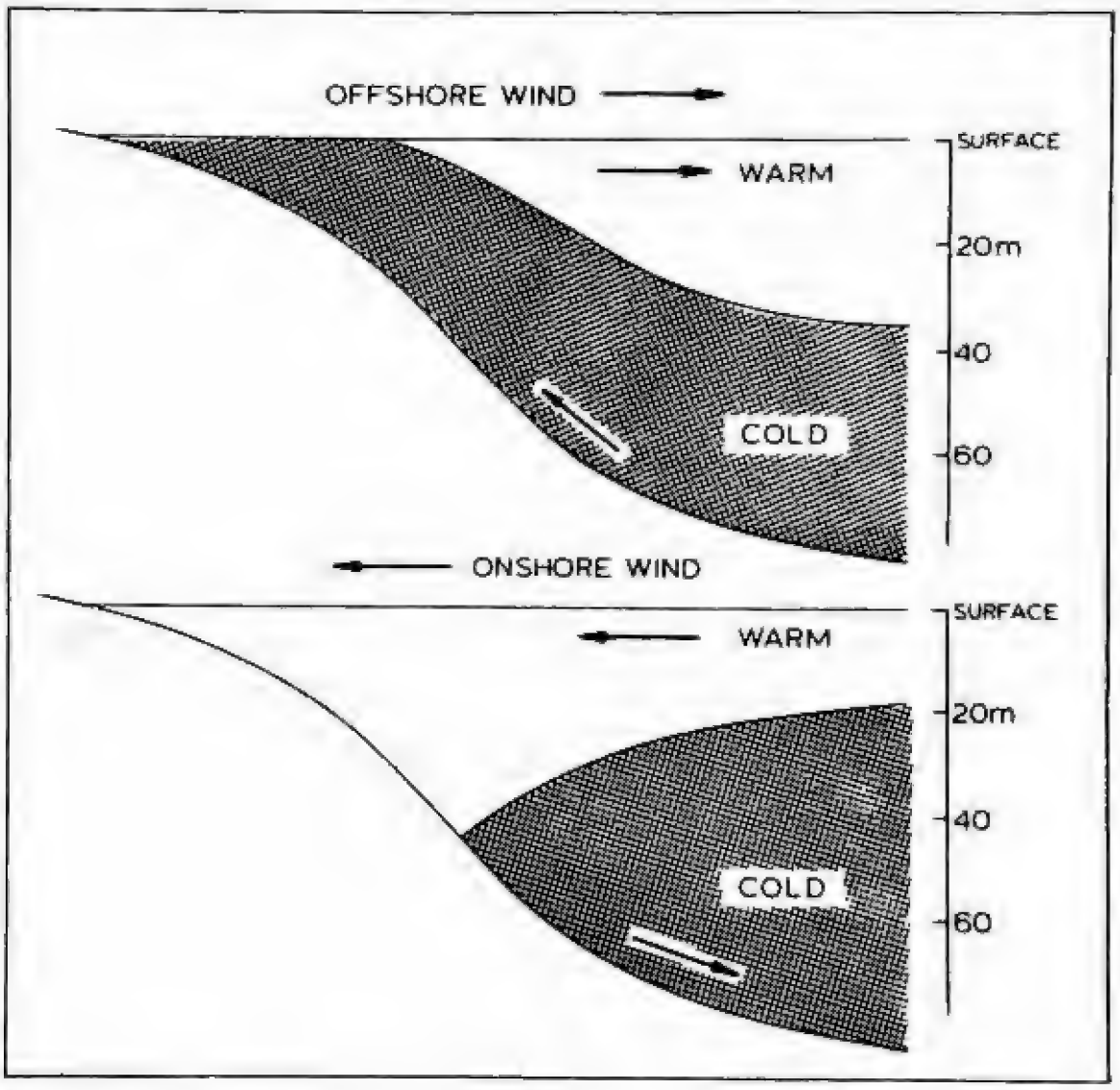


Figure 6

Schematic representation of the effect of offshore and onshore winds on the summer water temperatures and water layers in the nearshore zone along Newfoundland's east coast. (From Frank and Leggett 1982.)

Microscale Migrations: Onset of Larval Drift in Capelin

Reproductive success and recruitment in marine fish species that have pelagic larvae is highly variable (see Blaxter 1974, Dahlberg 1979, Lasker and Sherman 1981). The survival of larval stages of these species has long been considered a matter of chance. In years when the temporal and spatial distributions of concentrations of larvae and their prey are coincident, when the distributions of larvae and their predators are asynchronous, or both, survival is favored. When the opposite prevails, survival is poor (May 1974, Cushing 1975).

The location of spawning sites and the timing of reproduction in these species is often stock-specific, and is thought to be linked, through natural selection, to the probability of occurrence of favorable predator/prey fields (Cushing 1975; Cushing and Walsh 1976; Jacquaz, Able and Leggett 1977; Iles and Sinclair 1982). The stock-specific reproductive migrations of adults of these species, while less precise than those of shad and other anadromous species, presumably serve a similar role. The high recruitment variation in these species indicates, however, that these migrations are relatively ineffective in compensating for environmental stochasticity. Variation in several life history parameters and their correlates (age at maturity, fecundity, longevity, and energy allocation to growth and reproduction) are widespread and may conform to simple models of adaptive variation (Roff 1981, 1982, 1984).

The life history characteristics of capelin (***Mallotus villosus***) do not at first glance appear to conform to the predictions of theory even though their larvae are pelagic and experience extensive, passive transport by ocean currents (Jacquaz et al. 1977; Fortier and Leggett 1982, 1983). Northwest-Atlantic capelin spawn their eggs on gravel beaches at the heads of bays located along the eastern coast of Newfoundland and Labrador. Year class variation is substantial (Leggett, Frank and Carscadden 1984) but the frequency of repeat reproduction is low (<10%) and there is no evidence of intraspecific variation in age at maturity or fecundity over the considerable range of latitude at which spawning occurs (Templeman 1948). For the larvae of capelin, however, unlike most pelagic larvae, their association with favorable predator/prey conditions is far from accidental.

The physical and biological characteristics of the coastal water mass in eastern Newfoundland into which larval capelin emerge following hatching are strongly influenced by winds. Offshore (westerly) winds prevail. These westerly winds cause the warmer surface waters to be blown seaward and to be replaced by cold, subthermocline waters which upwell along the coast. Landward (easterly) winds are infrequent, unpredictable and generally of short (1−2 days) duration (Frank and Leggett 1982). They result from the passage of large-scale frontal systems along the coast (Leggett et al. 1984). Easterly winds cause the warm offshore surface waters to move landward, upwelling is arrested, and the coastal area becomes dominated by warm surface waters (Fig 6). The coastal replacement of cold upwelling waters with warm surface waters is rapid and dramatic, and occurs almost synchronously over the

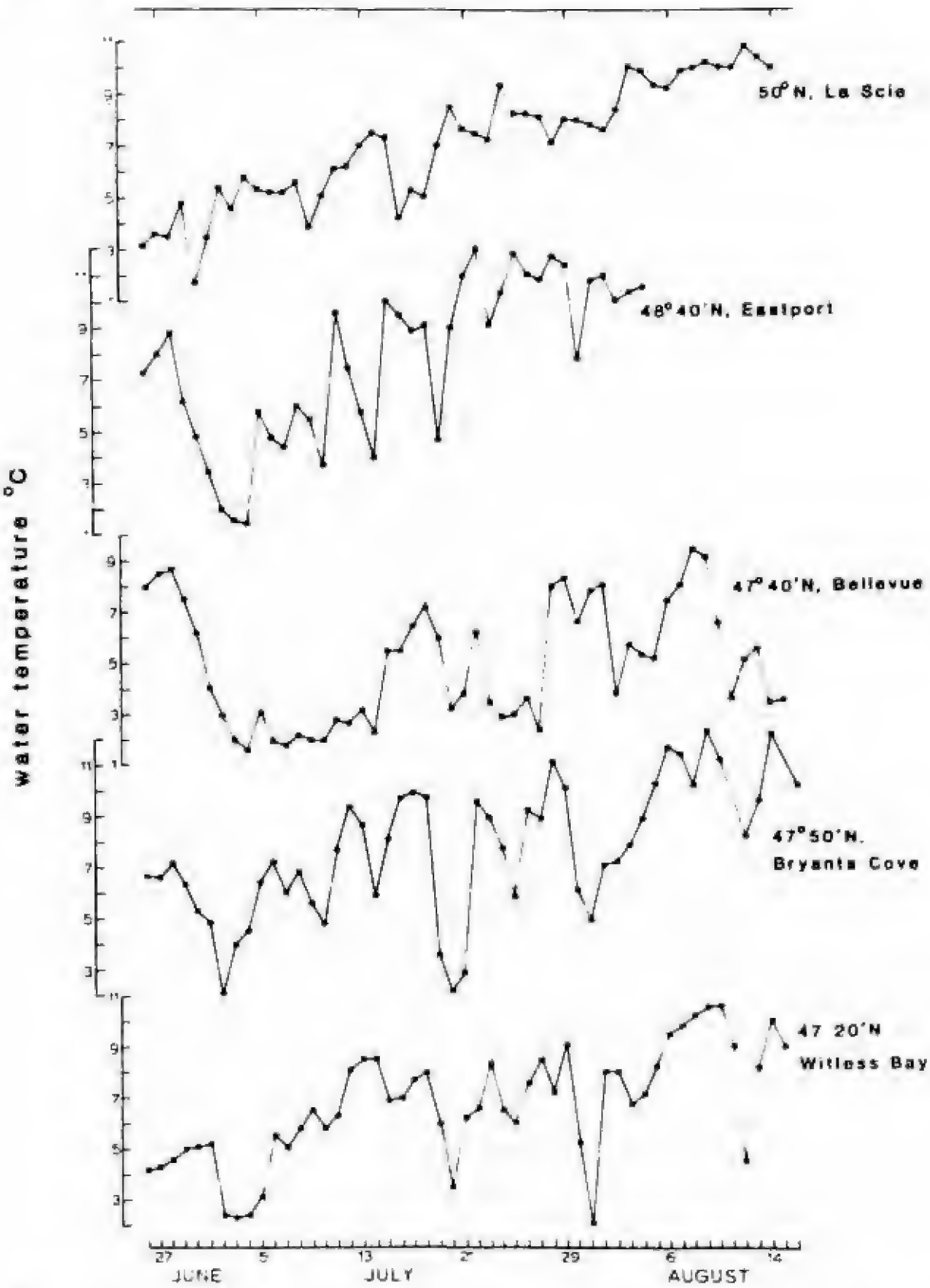
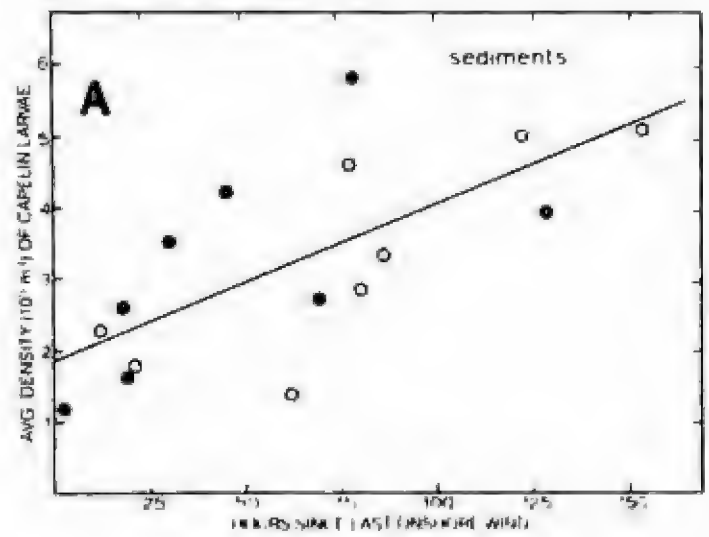


Figure 7

Synchronous wind-induced changes in nearshore water temperatures on the east coast of Newfoundland, 1982. Sharp temperature increases are coincident with onshore winds, falling temperatures with offshore winds. These wind patterns are generated by large scale weather fronts moving through the Newfoundland area. (From Leggett et al. 1984.)

entire east coast of Newfoundland (Fig 7).

The biomass of plankton in the 250 μ size range, the principal food of newly hatched larvae, is 2−3 times greater in the warm surface water mass, while the densities of chaetognaths and jellyfish, the principal predators of larval capelin during the early stages of drift, are 3−20 times lower in this water mass relative to the deep upwelling waters (Frank and Leggett 1982).



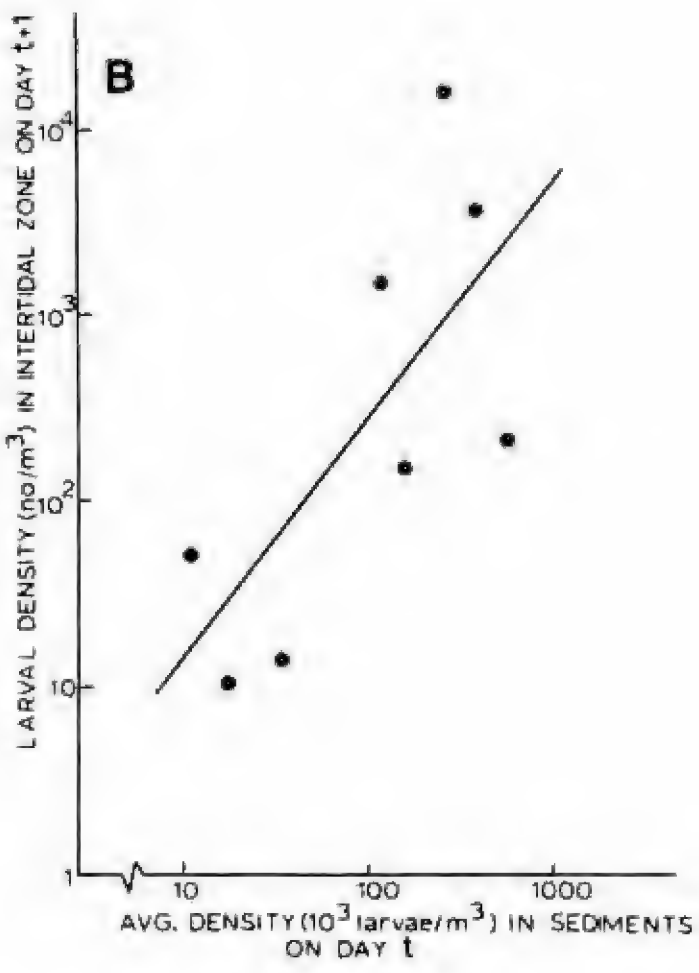


Figure 8

Increase in larval densities in the beach-spawning gravel as a function of the time since the last onshore wind (A) and the relationship between the density of larvae in the intertidal area one day after an onshore wind (t + 1) and the number of larvae in the sediments immediately prior to an onshore wind (day t)(B). (From Frank and Leggett 1981.)

High-frequency sampling of the beach gravel and the intertidal waters has revealed that capelin larvae accumulate in the top 20 cm of the beach gravel following hatching, and then emerge synchronously during onshore wind-induced coastal water mass exchanges (Fig 8). This synchronous emergence of capelin larvae causes them to become associated with, and concentrated in, water masses which are rich in food

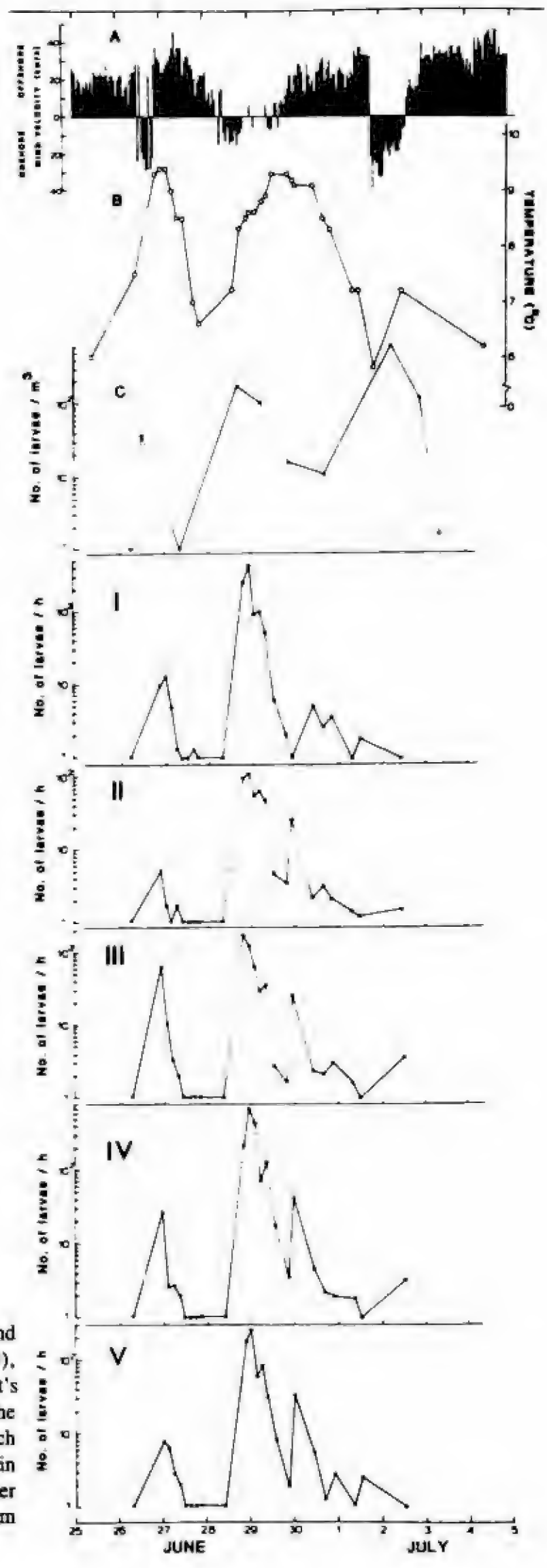


Figure 9

Relationship between wind direction and velocity (A), nearshore water temperature (B), intertidal densities of capelin larvae at Bryant's Cove, Newfoundland, 1981 (C), and the numbers of capelin larva that emerge from beach gravel within five aquaria which were located in a seaside laboratory and supplied with water pumped from the intertidal area (I-V). (From Frank and Leggett 1983b.)

and poor in predators.

To verify that this emergence pattern is active and hence adaptive, we isolated egg-bearing gravel in aquaria located in our Bryant's Cove, Newfoundland, laboratory. Filtered seawater, pumped directly from nearshore waters, was cycled into the tanks to duplicate the conditions experienced by eggs incubating in situ. The only difference between the tank and in situ conditions was the absence in the tanks of the wave-induced physical disturbance of the beach gravel which occurs during onshore winds and which could induce synchronous emergence through physical displacement of the larvae. Larval emergence in both the tanks and in situ was monitored daily and was related to the wind/water mass exchange patterns. The results (Fig 9) show that the patterns of larval emergence in all five aquaria, and in situ, were synchronous and corresponded precisely with sudden temperature increases induced by onshore wind-driven water mass exchange. This synchrony, in the absence of physical disturbances in the aquaria, clearly demonstrates that the episodic emergence of capelin larvae results to a considerable extent from active microscale migrations of the larvae in response to a reliable signal (presumably temperature) indicative of the occurrence of favorable predator/prey conditions. This finding is supported by our observation that significant larval emergence can occur in situ even during onshore wind events when wind velocities are too low to produce significant wave action but are sufficient to cause the expected temperature increase in the nearshore areas.

The accumulation of larvae in the beach sediments during offshore winds, and their subsequent synchronous emergence in response to wind-driven water mass exchange, results in periodic high densities of larvae in the nearshore area (Fig 10). Large volume (5 m^3) enclosure experiments in which the density of larvae and predators were manipulated to mimic natural densities, indicate that this active microscale migration from the gravel serves not only to place larvae in a favorable habitat, but may also result in predator satiation and a substantial reduction in the mortality rate immediately following emergence (Fig 11), when larvae would otherwise be most susceptible to predatory losses (Frank and Leggett 1982).

The temporal occurrence of predator-prey fields favoring early larval survival in capelin is thus unpredictable, as it depends on large-scale meteorological events. To this extent the larvae of capelin are potentially faced with environmental uncertainty not unlike that experienced by other fish species which have pelagic larvae. The association of favorable conditions with a reliable environmental signal—dramatic temperature increases caused by wind-driven water mass exchange—is, however, highly predictable. The active emergence of capelin larvae from the beach gravel in response to this signal, achieved by a synchronized microscale migration of less than one meter, greatly dampens the stochastic nature of the predator-prey field actually experienced by the larvae of capelin.

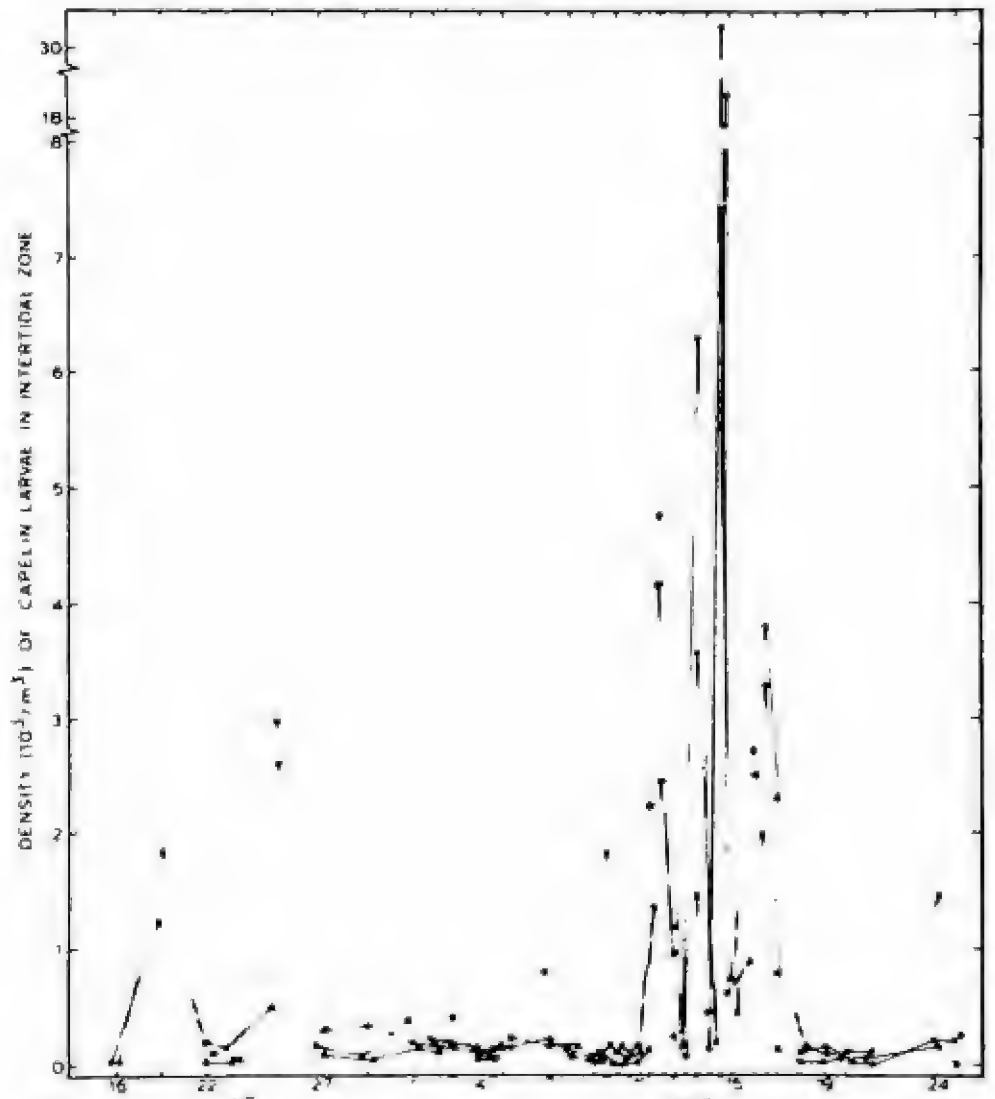


Figure 10

Pattern of appearance of larval capelin in the intertidal zone at three stations adjacent to the spawning beach at Bryant's Cove, Newfoundland, 1978. Peaks in larval abundance correspond to times of onshore winds. (From Frank and Leggett 1981.)

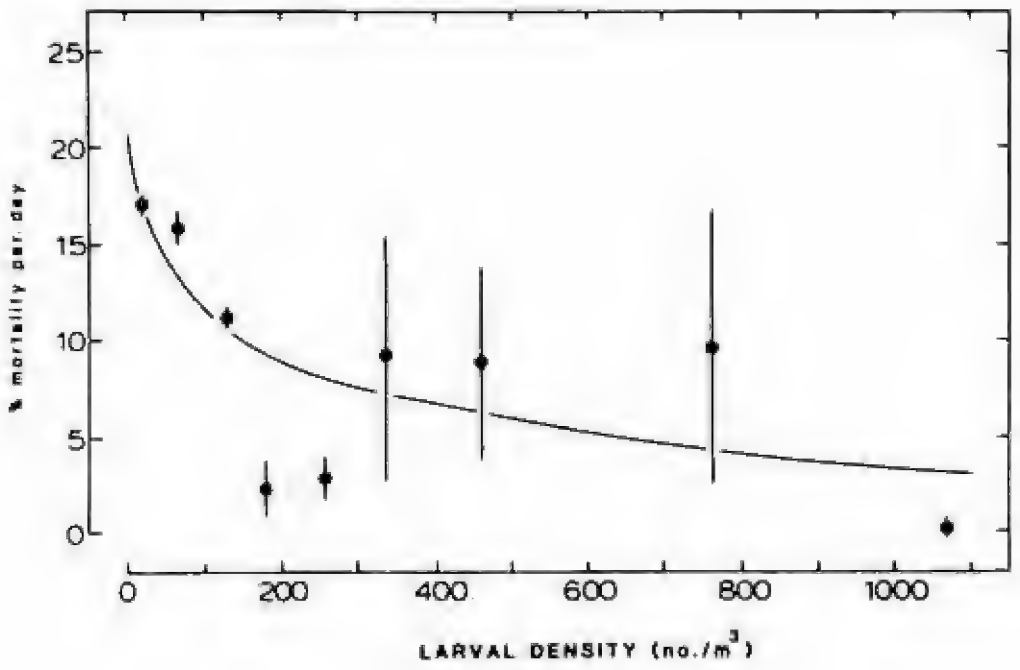


Figure 11

Relationship between percent mortality per day experienced by capelin larvae due to predation by ctenophores, and larval density. Means and ranges shown. (From Frank and Leggett 1982.)

The environmental variability actually experienced by the larvae of capelin is thus quite similar in general form to that experienced by southern shad populations even though the potential variance differs dramatically. When viewed in this way, the similarities in their life history traits are more readily understood and are consistent with theory. The larvae of many pelagic spawning fish species, which are a part of the plankton throughout their entire larval period, are, in contrast, less able to regulate the environmental field to which they are exposed because their ability to regulate their distribution vis-a-vis predator/prey abundances in a predictable way is restricted. The selective pressures experienced by these species are then akin, in many ways, to those experienced by members of northern shad populations, and their life history patterns also conform to the predictions of theory.

It has recently been shown (Frank and Leggett 1983a) that the appearance of the larvae of several other nearshore demersal spawners in the plankton is also synchronous with coastal water mass exchange in eastern Newfoundland and with the emergence of capelin. Fortier and Leggett (1982, 1983, 1984) have also recently demonstrated that microscale migrations of larval herring (*Clupea harengus*), which influence their association with different current regimes, are important to their retention in food-rich areas of the upper St. Lawrence estuary. Similar findings have recently been reported by Graham (1972); Weinstein, Weiss, Hodson and Gerry (1980); Melville-Smith, Baird and Wooldridge (1981) and Miller, Crowder and Moser (1985).

These findings suggest that microscale migrations of larval fishes may be more widespread than previously believed and a significant factor in the active association of these early larval stages with favorable habitats, the distribution of which is variable in time and space. The extent to which these migrations are instrumental in moderating the impact of environmental variables on reproductive success is not yet well defined. Studies with capelin indicate that up to 58% of the year-to-year variation in reproductive success may be attributable to the extent to which larval emergence is successfully linked to water mass exchange (Leggett et al. 1984).

CONCLUSIONS

The observations reported above are far from exhaustive. They do indicate, however, that the nature of environmental variance, and of the behavioral responses of animals to that variance, can play a major role in the evolution of life history traits. It is no longer sufficient, then, to assume that because one or more parameters known to be relevant to reproductive success are stochastic in time or space, particular life history patterns should be expressed. The important question, in this context, is whether this variability is actually experienced by the species. As the detailed analyses of the macro- and microscale migrations of shad and capelin have shown, appropriate behavioral responses by individual fishes to reliable environmental signals can greatly reduce the environmental uncertainty actually experienced. Under these circumstances, selection for adaptations at the life history level may be greatly reduced. The data for American shad and for Atlantic salmon (Schafer and Elson

1975) indicate that where behavioral adaptations are incapable of stabilizing this variance, life history traits consistent with the predictions of theory will evolve. The extent to which migratory behavior and other behaviors are successful in moderating reproductive variance can be expected to have a major influence on the evolution of other life history traits, such as fecundity, frequency of reproduction, and age at maturity. Students of life history traits should, therefore, take greater care to consider macro- and microscale migrations and other behavioral adaptations when evaluating the degree of correspondence, or lack thereof, between observed patterns in life history parameters and the predictions of theory.

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COMPARATIVE MIGRATORY AND REPRODUCTIVE STRATEGIES OF THE SYMPATRIC ANADROMOUS COREGONINE SPECIES OF JAMES BAY

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ABSTRACT

Anadromous cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) represent a major faunal component of the estuarine fish communities of the east coast of James-Hudson Bay. Cisco dominate in the south of this range but decline in relative abundance northwards, suggesting that physiological constraints related to a restricted energy budget overwhelm expected coadapted life history traits. In the present study, the energetic costs of reproduction, migration and overwintering of cisco and whitefish and the energetic efficiency of their migratory behavior was quantified and compared. This comparison was made to test the hypothesis that if cisco bear proportionately greater reproductive and survival costs, they may then exhibit an energetically more efficient mechanism of migration than whitefish such that energy savings could be invested in either reproduction or survival. In the Eastmain river, cisco exhibit greater reproductive effort and greater post-spawning mortality than do whitefish. The somatic cost of the freshwater migration is proportionately smaller for cisco than for whitefish, despite the observation that whitefish feed in the river. However, cisco do not behave so as to minimize energy expenditures during the upstream migration. We propose that those factors which augment energy expenditures are related to environmental constraints that require cisco to spend long periods of time in the spawning river away from feeding grounds. The prolonged and meandering migration exhibited by both species in the river is discussed relative to present theories of optimal migratory behavior.

INTRODUCTION

The estuaries and rivers which drain the eastern coasts of James and Hudson Bay (Fig 1) are home to or are utilized by some 38 species of fish belonging to 15 families (Morin, Dodson and Power 1980). A major faunal component of these estuarine fish communities is represented by two anadromous coregonines, the cisco (*Coregonus artedii*) and the lake whitefish *(C. clupeaformis)* (Morin et al. 1980, Lambert and Dodson 1982a). The relative abundance of the two species changes along the coastline, with cisco dominant in the south of the range and whitefish in the north.

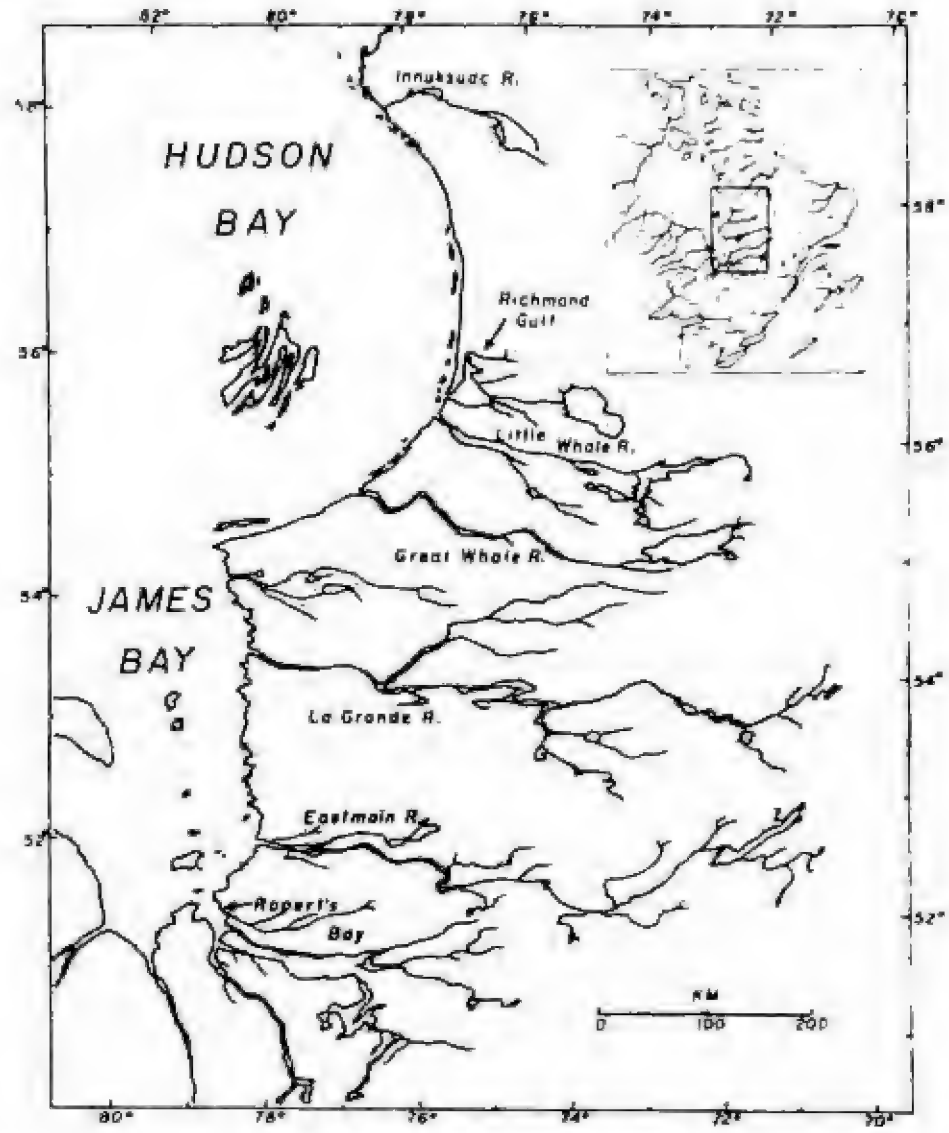

Figure 1
Location map of the east coast of James and Hudson bays.

The Innuksuac River represents the northern limit of cisco. This gradient in relative abundance is associated with a change in climate along the coastline. The growing season (mean daily temperature > 5.6°C) ranges from 140 d at Rupert's Bay to 80 d at the Innuksuac River (Wilson 1971).

Cisco and whitefish exhibit different life history characteristics within any one river system. In the La Grande River, located near the middle of the James-Hudson Bay coastal range, whitefish attain greater maximum age, greater size, and later age at maturity, whereas cisco exhibit a greater rate of growth prior to reproduction and higher fecundity (Morin, Dodson and Power 1982). Both species, although iteroparous, do not spawn yearly once maturity is reached. This phenomenon of skipping annual reproductive events has been related to the cost of accessory reproductive activities (e.g., migration) in poor habitats (Bull and Shine 1979).

Both species exhibit a latitudinal gradient in life history characteristics over their James-Hudson Bay range. Lake whitefish exhibit reduced reproductive effort independent of changes in growth northwards over their James-Hudson Bay coastal range. In the case of cisco, however, both growth and reproductive effort are reduced northwards over their coastal range (Morin et al. 1982).

Similar comparisons of fish populations have demonstrated latitudinal variations in life history tactics. Several authors have noted a general trend among northern fishes to reduce fecundity and increase the lifetime frequency of spawning (Nikolskii 1970, Leggett and Carscadden 1978). Several hypotheses have been proposed to explain these observations (briefly reviewed by Morin et al. 1982). From an evolutionary perspective, there may be a trade-off in energy allocation between growth, maintenance and reproduction that maximizes the individual's contribution to future generations. In the shorter growing season of the north, reduced fecundity may be an adaptation to ensure an adequate allocation of energy from a restricted energy budget to maintenance and growth. Reduced fecundity may be balanced by an increase in longevity which could permit more reproductive cycles. Although such evolutionary interpretations are conceptually appealing, Nikolskii (1969) and Bagenal (1978) have cautioned against assuming adaptive significance in intraspecific life history variations because of the effects of such proximal factors as temperature and food on growth, maturation and fecundity.

Life history variations of the anadromous coregonines of James-Hudson Bay do not clearly conform to evolutionary interpretations, particularly in the case of cisco. As cisco reach the northern limit of their range in Hudson Bay, reduced growth may occur because of shorter growing seasons; reproductive maturation may be delayed due to reduced growth. The fecundity of cisco, which remains unchanged along the coast, may already be minimal and the increased skipping of annual reproductive events observed in the north may represent one way in which reproductive effort can be reduced beyond a minimal fecundity. Thus these changes may not represent adaptive changes but physiological responses to a decreasing energy budget whereby further trade-offs in energy allocation are not possible. In this case, life-history strategies are not free to evolve under the purely demographic forces of selection. Physiological constraints may overwhelm expected coadapted life history traits (Morin et al. 1982).

Migration is an obvious and essential component of the life cycle of these fish and must be accounted for in any theory concerning life history strategies and energy budget partitioning. In the Eastmain and La Grande Rivers, the spring hatching period of both species coincides with spring thaw, and larvae are flushed from the rivers into James Bay (Ochman and Dodson 1982). During the months of September and October, juveniles and nonreproductive adults enter the lower reaches of the rivers where they pass the winter. During the following spring, all fish of both species leave the rivers, following the receding pack ice for their feeding migration in James Bay. The upstream migration of mature fish begins in mid- to late July. Whitefish spawn at the base of rapids in mid-October at temperatures of approximately 5°C, whereas cisco spawn in the same areas in early November as the rivers freeze (Morin, Dodson and Power 1981).

The theoretical basis of our research program, of which this is a status report, is that migration and reproduction are functionally related through the partitioning of a limited energy resource and that the costs and benefits of migration may be empirically equated to reproductive effort and survival. Our approach to this hypothesis is a comparative one; the reproductive and migratory patterns of two

closely related sympatric species are compared within the same set of environmental conditions (the Eastmain River). Whereas whitefish appear physiologically capable of pursuing a more or less predictable evolutionary trajectory in life history, northwards over their James-Hudson Bay coastal range, cisco appear unable to do so. Thus, the procedure is to consider whitefish as a standard with which cisco can be compared in order to answer the following question: if cisco must bear proportionately greater reproductive and survival costs related to the shorter growing seasons in the north, do they exhibit an energetically more efficient mechanism of migration whereby energy savings could be invested in either reproduction or survival. The present study reports on our progress to date in the quantification and comparison of the energetic costs of reproduction, migration and overwintering of cisco and whitefish. On the basis of experimental fishing studies and the tracking of sonic-tagged fish, we also examine the relationship of the above variables to the energetic efficiency of migratory behavior in these fish.

MATERIALS AND METHODS

Seasonal migration patterns of cisco and whitefish were documented between 1979 and 1981 by recording changes of catch per unit effort and in length composition of gill net samples obtained from mid-May (spring thaw) to late October (winter freeze-up) in the Eastmain River and adjacent areas (Lambert and Dodson 1982b). The discharge of the Eastmain River was reduced by approximately 85% in July 1980 as part of the James Bay hydroelectric scheme. The effect of this reduction in freshwater outflow was to reduce the residual current in the estuarine portion of the river (below first rapids, Fig 2) from 40 cm $\cdot s^{-1}$ to approximately 5 cm $\cdot s^{-1}$, thus extending the zone of reverse tidal flow up to the first rapids. This change, however, did not significantly alter the seasonal migration pattern of either species (Lambert and Dodson 1982b). Therefore, catch per unit effort data were pooled by region and sampling date for 1979 to 1981 to establish a general migratory route for each species based on changes in abundance.

The comparative costs of migration and reproduction were documented by quantifying the absolute weight change of gonads, digestive system, liver and muscle tissue of adults sampled along their general migratory route. Adults were defined as fish which exceeded the mean fork-length at first reproduction, 26 cm in the case of cisco and 32 cm in the case of whitefish. Analysis of the energetic content of these tissues, as a direct measure of energy partitioning strategies, is presently underway, but tissue weight changes are a good indication of energy utilization. Glebe and Leggett (1981) found that changes in tissue mass closely paralleled changes in tissue energy content in the case of American shad *(Alosa sapidissima)*. Ten reproductive and 10 nonreproductive adults of each sex and each species were sampled whenever possible from May 1982 to May 1983 according to the following schedule: (a) spring break-up (15–30 May 1982) at the mouth of the Eastmain River (Fig 2) during the seaward migration of both species following the overwintering period; (b) mid-July along the coast and in the vicinity of islands situated 15–20 km north of the river

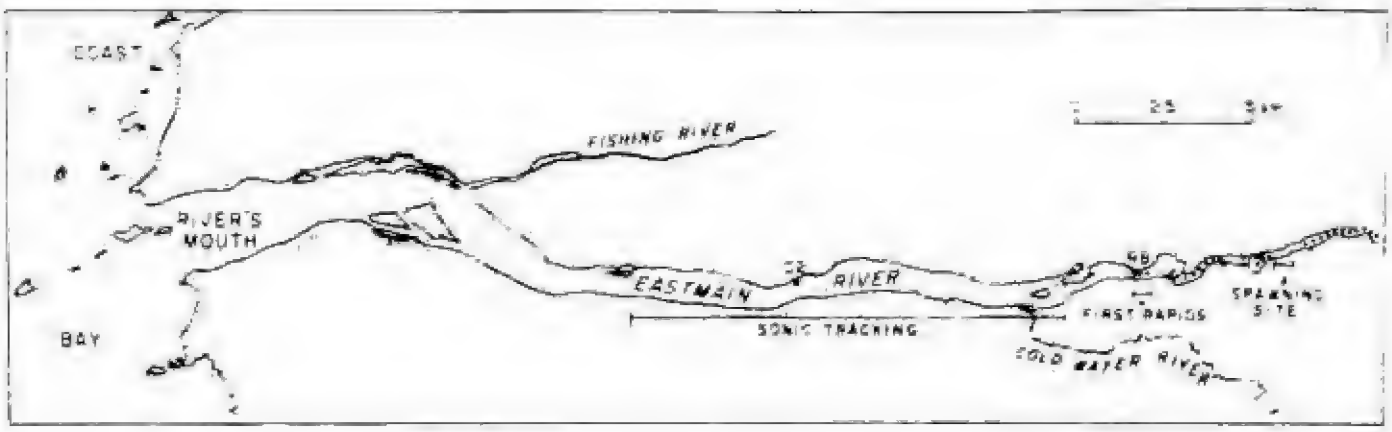

Figure 2

Location map of the Eastmain River. Sampling stations for the study of upstream migration are indicated (C2, RB) as is the section of the river where sonic tracking experiments were conducted. Arrows indicate rapids.

during the feeding migration of both species; (c) mid-August at the mouth of the Eastmain River for the return migration of spawning adults and along the coast north of the river (Fig 2) for nonreproductive adults; (d) mid-September at the base of the first rapids (Fig 2) for mature adults and along the coast for nonreproductive adults; (e) mid-October on the spawning grounds for mature adults and at the river's mouth for nonreproductive adults; (f) early November on the spawning grounds for spent fish; (g) spring break-up (May 1983) at the river's mouth to complete one annual cycle. Spent fish captured in the spring of 1983 are identified in the results as "reproductive" individuals relative to the 1982 season. Similarly, fish captured in the spring of 1983 and identified as potential spawners are identified as "nonreproductive" individuals relative to the 1982 season.

Nonreproductive females were identified in the spring of 1982 by the presence of unresorbed eggs and flaccid appearance of the ovaries. The identification of nonreproductive males in the spring of 1982 was more subjective and based on the flaccid appearance of the testes. For the rest of the season, maturity stages and the gonadosomatic index (weight of gonads as a proportion of body weight) were used to differentiate between reproductive and nonreproductive fish. As age and length at maturity are highly variable in both species (Morin et al. 1982), it is probable that fish identified as nonreproductive include repeat spawners that had skipped spawning, and late-maturing virgin fish.

Changes in weight of different tissues at successive stages in the migration were quantified by calculating linear regressions of tissue weight on length (logarithmic transformed data) for reproductive and nonreproductive adults of each species at each sampling site along the migratory route and comparing significant linear regression by analysis of covariance (Sokal and Rohlf 1981). Absolute weight changes for each tissue were determined from the linear regressions at each sampling site for standard fish of each species. A standard fish corresponds to the observed mean length of reproductive adults of each species, 29 cm in the case of cisco and 36 cm in the case of whitefish.

The costs of reproduction and migration for each species were calculated by comparing the somatic and reproductive investments of reproductive females captured at various sites along the migratory route to those of nonreproductive females of the same length sampled at the same time using the parameters defined by Tuomi, Hakala and Haukioja (1983):

I_n = the somatic investment of nonreproductive fish
I_s = the somatic investment of reproductive fish
I_r = the reproductive investment of reproductive fish
I_a = the total investment of reproductive fish ($I_s + I_r$)

The parameters used in comparing reproductive and migratory costs of cisco and whitefish are defined in absolute terms as follows:

I_n = net dry weight (muscle + liver + digestive tract) of nonreproductive fish sampled during the spawning season, 1982.
$I_{n''}$ = net dry weight of nonreproductive fish surviving in the spring of 1983 sampled at the river's mouth.
I_s = net dry weight of reproductive fish sampled during the spawning season, 1982.
$I_{s'}$ = net dry weight of reproductive fish sampled at the river's mouth prior to upstream migration, August 1982.
$I_{s''}$ = net dry weight of reproductive fish surviving in the spring of 1983 sampled at the river's mouth.
I_r = dry weight of gonads of reproductive fish sampled during the spawning season, 1982.
$I_{r'}$ = dry weight of gonads of reproductive fish sampled at the river's mouth prior to upstream migration, August 1982.
I_a = total dry weight of reproductive fish sampled during the spawning season, 1982.

Dry tissue weights were used in all calculations to avoid any bias due to fluctuating moisture content. As our own analyses are not yet complete, we used moisture content values published for ***Coregonus albula*** (Dabrowski 1982). Moisture content varies from 72% to 80% of somatic tissue weight and from 60% to 70% of gonad weight depending on time of the year and the extent of gonad development.

The absolute amount of resources produced by differences in resource input between reproductive and nonreproductive individuals is given by

$$R_a = I_a - I_n \tag{1}$$

The proportion of increased resource input from the total investment of reproductive individuals is given by

$$RE_a = \frac{R_a}{I_a} \tag{2}$$

Reproductive effort is given by

$$R_e = \frac{I_r}{I_a} \tag{3}$$

Differences in reproductive effort between the two species were also documented by regressing fecundity on net body weight (logarithmic transformed data) for each species and comparing regression lines by analysis of covariance.

The absolute cost of the spawning migration in the Eastmain River was estimated by calculating the somatic weight loss which reproductive fish incurred between the time of river entry in August and spawning in October; from that value was subtracted the increase in gonad weight for the same period. Expressing this cost as a proportion of the somatic investment of reproductive fish prior to upstream migration, migratory effort is given by

$$M_e = \frac{(I_{s'} - I_s) - (I_r - I_{r'})}{I_{s'}} \tag{4}$$

Reproduction and migration could result in survival costs when somatic costs increase the vulnerability of spent fish to winter mortality. The relative cost of overwintering of nonreproductive and reproductive fish was estimated as the weight loss exhibited by the two groups surviving in the spring of 1983 as a proportion of their total somatic investment. In the case of nonreproductive fish, overwintering effort is given by

$$W_n = \frac{(I_n - I_{n''})}{I_n} \tag{5}$$

In the case of reproductive fish, overwintering effort is given by

$$W_r = \frac{(I_s - I_{s''})}{I_s} \tag{6}$$

It is most likely that overwintering mortality is selective in that both reproductive and nonreproductive fish in the poorest condition suffer the greatest mortality. As a result, W_r and W_n are probably underestimated; the greater the mortality of fish during the winter, the smaller the value of W_r (or W_n). Thus the absolute values of W_r and W_n for both species are biased estimates of the cost of overwintering. Comparatively speaking, however, if $W_r = W_n$, it is assumed that nonreproductive and spent fish of the same species are equally vulnerable to mortality and that migration and reproduction do not result in survival costs. If $W_r < W_n$, it is assumed that spent fish suffer greater mortality relative to nonreproductive fish. In this case, migration and reproduction result in survival costs.

Differential survival of cisco and whitefish of reproductive size was examined by grouping the entire 1980 catch of each species into size classes of equal breadth and plotting log frequency against size (catch curves; Ricker 1975). The 1980 catch was used as it was our most complete fishing effort and was considered most representative of the entire population. The descending right limb of the catch curve is an indication of mortality rate. The steeper the right limb, the greater is the mortality rate.

The upstream migration of cisco and whitefish in the Eastmain River was investigated in 1983. Rate of upstream displacement was estimated from the catches of two gill nets measuring 45.7 × 1.8 m composed of 3 panels of multifilament mesh graded 64, 76 and 89 mm (stretched measure), selective for fish of reproductive size. One gill net was installed at the base of the first rapids (station RB, Fig 2) from July 13 to September 6 and the second installed 8 km downstream (station C2, Fig 2) from August 2 to September 6. Nets were visited daily, and all captures were measured, sexed and the presence of stomach contents noted.

Ten whitefish and 5 cisco were tagged externally with ultrasonic transmitters and tracked continuously in order to document migratory behavior. The tags had a frequency of 69 KHz and measured 3.5 cm in length and 0.75 cm in diameter. Three whitefish and two cisco were captured at the first rapids and displaced downstream to station C2 for release; the remaining fish were captured and released at station C2. Fish were tracked individually from a 17-foot inflatable boat equipped with a manually rotated directional hydrophone and positioned every 30 minutes with a microwave positioning system. The current speed and direction at the surface and on the bottom were also recorded at these positions. Two continuously recording Aandera current meters were moored at the upstream and downstream end of the tracking zone to provide supplementary current data. These data were combined and used together with observations of fish movement over time to calculate swimming speed through the water by use of vector velocity techniques.

The energetic efficiency of the migratory behavior of cisco was evaluated by comparing observed swimming speeds to the optimum speeds of fish swimming in currents as predicted by the model of Trump and Leggett (1980). This model predicts that to minimize the energy cost of migration per unit distance in areas of variable currents, fish should ignore variations in current and maintain a constant speed through the water equal to $U_o + \frac{1}{b}$, where U_o is the residual current of the river (5 cm $\cdot s^{-1}$ in the estuarine portion of the Eastmain River) and b is a constant in the equation describing the relationship between specific energy expenditure per unit time and swimming speed as elaborated by Brett (1964). This constant is empirically evaluated and varies according to the morphology, length and physiological condition of the fish. As b has not yet been evaluated for cisco, we have used the value $b = 3.71$ s $\cdot m^{-1}$ evaluated for a 30 cm rainbow trout *(Salmo gairdneri)* by Webb (1971). This length approximates the length of our standard cisco (29 cm).

We are unable to repeat this analysis for whitefish. The model of Trump and Leggett (1980), which is based on an approach first presented by Weihs (1973), assumes that no feeding, evacuation or growth takes place during the period of swimming being analyzed. Thus the only significant contributions to energy flux are due to locomotion and basal metabolism (Weihs 1984). As 54% of the whitefish sampled at the first rapids possessed full stomachs, this fundamental assumption is not respected.

Table 1

Analysis of covariance for the regressions of net weight and total weight with length (log-transformed data) for the cisco (*Coregonus artedii*) sampled along their migratory route with the degrees of freedom (d.f.), the F-value (F) and the probability level (p) for the test of homogeneity of slopes and elevations if no significant differences exist between slopes ($p > 0.01$). The degrees of freedom are $a-1, n-2a$ for the test of slopes and $a-1, n-a-1$ for the test of elevation where a is the number of regressions and n the number of individuals.

	Reproductive Males			Nonreproductive Males		
	d.f.	F	p	d.f.	F	p
Net Weight						
Slope	4,32	3.06	0.030	2,25	2.12	0.141
Elevation	4,35	5.34	0.002	2,27	27.83	< 0.001
Total Weight						
Slope	4,32	3.03	0.031	2,25	2.08	0.145
Elevation	4,36	6.51	< 0.001	2,27	26.77	< 0.001
	Reproductive Females			**Nonreproductive Females**		
	d.f.	F	p	d.f.	F	p
Net Weight						
Slope	6,51	1.39	0.235	3,30	0.72	0.548
Elevation	6,57	16.75	< 0.001	3,33	26.27	< 0.001
Total Weight						
Slope	6,51	0.93	0.484	3,30	0.78	0.512
Elevation	6,57	10.99	< 0.001	3,33	24.66	< 0.001

RESULTS AND DISCUSSION

Cisco sampled along their migratory route in 1982 exhibited significant changes in total and net weight in the case of reproductive and nonreproductive individuals of both sexes (Table 1). The analysis of absolute changes in total and net weight of standard male and female cisco (Fig 3) indicates that nonreproductive individuals accumulate somatic weight throughout the growing season and that this accumulated reserve is subsequently invested by reproductive individuals in gonads and accessory reproductive activities. In the case of female cisco, this accumulated reserve represents 15.7% of the total weight of reproductive individuals (RE_a, Table 2). Female cisco invest 25.6% of their total weight in gonads (R_e, Table 2). The reduction in total weight of reproductive fish due to spawning and overwintering suggests that spent fish surviving in the spring of 1983 (Fig 3) must accumulate somatic weight during at least one growing season before adequate reserves are available for repeat spawning.

Table 2

Summary of the parameters used to compare the costs of reproduction, migration and overwintering of female cisco and whitefish. Parameter values are given as percentages. See text for definitions of parameters.

Parameter	Cisco	Whitefish
RE_a	15.7	11.8
R_e	25.6	22.0
W_n	5.0	9.0
W_r	0.0	10.0
M_e	28.0	35.0

Whitefish also exhibited significant changes in total and net weight along their migratory route, except in the case of reproductive males (Table 3). The analysis of absolute changes in the net and total weight of females (Fig 4) revealed a pattern similar to that observed for cisco whereby nonreproductive individuals accumulate somatic weight throughout the growing season and subsequently invest it in gonads and accessory reproductive activities. However, this accumulated reserve, which represents 11.8% of the total weight of the reproductive female whitefish, appears to be less important in whitefish than in cisco (RE_a, Table 2). Furthermore, the reproductive effort of female whitefish is less than that of cisco; whitefish invest 22% of their total resources in gonads (RE_a, Table 2). This lower reproductive effort is also reflected in a significantly lower fecundity for whitefish compared with cisco (Table 4).

The reduction in total weight of reproductive females due to spawning and overwintering is proportionately less acute for whitefish than for cisco. Although the somatic weight of spent females surviving in the spring of 1983 was significantly lower than that of females that did not spawn in 1982, this difference was not evident in the spring of 1982 (Fig 4). This may be the result of interannual differences in resource accumulation and expenditure. This, in combination with the observation that female whitefish invest proportionately less weight in gonads and are less dependent on reserves accumulated during nonreproductive years than cisco, suggests that an unknown proportion of female whitefish may be capable of spawning in successive years. In the case of male whitefish, no obvious differences in weight exist between reproductive and nonreproductive fish throughout the season (Fig 4). Most males are apparently capable of spawning annually once sexual maturity is attained. Non-reproductive males sampled in this study are most likely late-maturing virgin fish.

The analysis of weight loss due to overwintering suggests that reproductive female cisco experience greater mortality during the winter following spawning than do whitefish. Whereas surviving nonreproductive female cisco lose 5% of their somatic weight during the winter (W_n, Table 2), surviving spent fish apparently lose no weight (W_r, Table 2). As this is obviously impossible, we propose that spent fish suffer greater mortality than do nonreproductive individuals and that only spent fish in

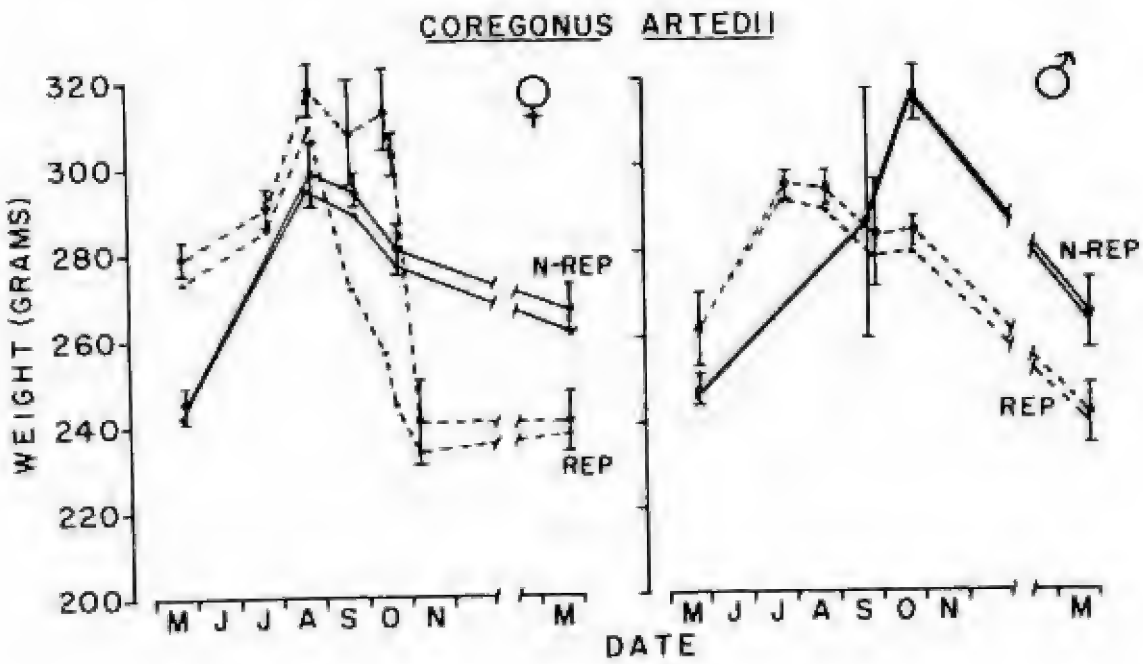

Figure 3

Total and net weight of standard reproductive (REP, dashed lines) and nonreproductive (NREP, solid lines) cisco sampled from May to November, 1982, and in May, 1983 along their migratory route. In the case of both REP and NREP fish, upper line indicates total weight, lower line indicates net weight. Vertical bars indicate standard deviations of total weight derived from regression analyses of total weight/body length relationships.

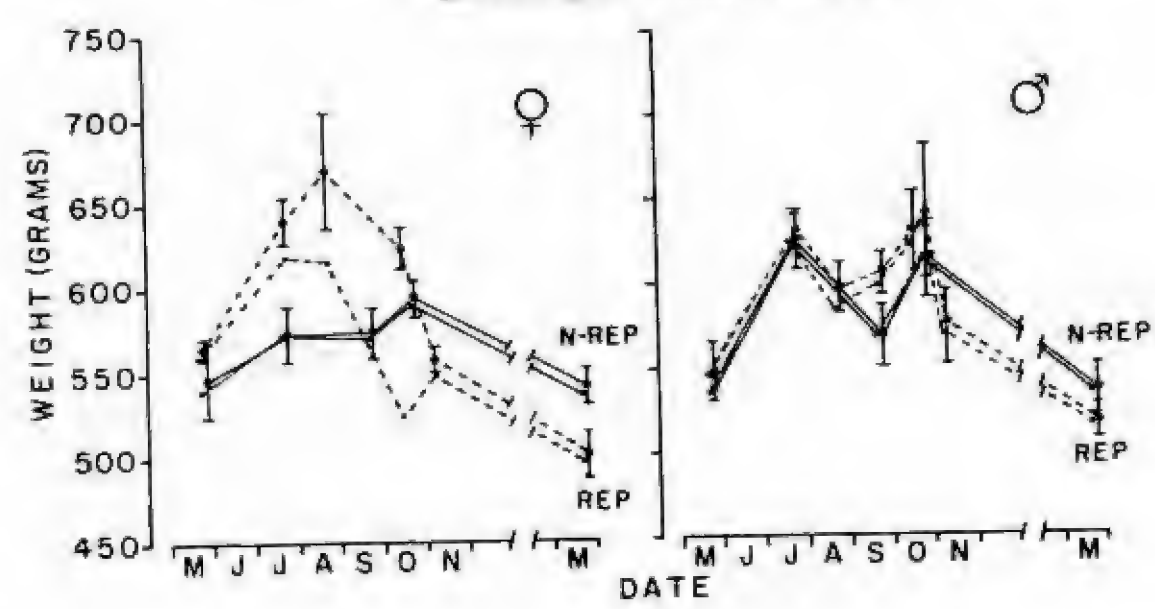

Figure 4

Total and net weight of standard reproductive (REP, dashed lines) and nonreproductive (NREP, solid lines) whitefish sampled from May to November, 1982, and in May 1983, along their migratory route. In the case of both REP and NREP fish, upper line indicates total weight, lower line indicates net weight. Vertical bars indicate standard deviations of total weight derived from regression analyses of total weight/body length relationships.

Table 3

Analysis of covariance for the regressions of net weight and total weight with length (log-transformed data) for the whitefish (*Coregonus clupeaformis*) sampled along their migratory route with the degrees of freedom (d.f.), the F-value (F) and the probability level (p) for the test of homogeneity of slopes and elevations if no significant differences exist between slopes ($p > 0.01$). The degrees of freedom are $a-1$, $n-2a$ for the test of slopes and $a-1$, $n-a-1$ for the test of elevations where a is the number of regressions and n the number of individuals.

	Reproductive Males			Nonreproductive Males		
	d.f.	F	p	d.f.	F	p
Net Weight						
Slope	6,39	1.38	0.244	3,25	1.20	0.329
Elevation	6,45	1.79	0.123	3,28	11.30	< 0.001
Total Weight						
Slope	6,39	1.39	0.241	3,25	1.21	0.327
Elevation	6,45	2.06	0.077	3,28	11.08	< 0.001
	Reproductive females			**Nonreproductive Females**		
	d.f.	F	p	d.f.	F	p
Net Weight						
Slope	5,47	2.55	0.040	3,25	2.78	0.061
Elevation	5,52	9.29	< 0.001	3,28	5.49	0.004
Total Weight						
Slope	4,43	3.87	0.009	3,25	2.77	0.062
Elevation	—	—	—	3,28	4.83	0.008

the best condition are able to survive the winter. In the case of whitefish, weight losses of surviving spent and nonreproductive fish are similar (Table 2), suggesting that female whitefish invest resources in survival that are not available for reproduction.

Evidence in support of the hypothesis that cisco suffer greater mortality due to reproduction than do whitefish is provided by the analysis of catch curves (Fig 5). The interpretation of the catch curves (Ricker 1975), in the case of whitefish, indicates a low mortality rate in combination with a diminishing growth rate that causes the piling-up and apparent increased abundance of reproductive fish (> 32 cm) relative to smaller length classes. The cisco catch curve indicates a high mortality rate following the attainment of the mean length at maturity (26 cm) in combination with a diminishing growth rate, that causes a steeply descending right limb of the curve. As our age-length analyses are incomplete, we are unable to calculate absolute mortality rates. Comparatively speaking, however, our preliminary conclusion is that cisco exhibit higher post-spawning mortality than do whitefish.

Table 4

Regressions of the logarithm of fecundity (y) on the logarithm of net body weight (x) for cisco and lake whitefish sampled in 1979 and 1980 in the Eastmain River n = number of fish sampled, F = F-value for the significance of the regression; p = probability level of significance. An analysis of covariance showed that the slopes did not differ significantly ($F = 2.06$, $p < 0.154$) but that the adjusted mean fecundities were significantly different ($F = 7.28$, $p < 0.008$).

Species	Regression Equation	n	F	p
Cisco	$y = 0.851 + 1.243x$	43	42.98	< 0.0001
Lake Whitefish	$y = 1.892 + 0.798x$	44	10.91	< 0.0025

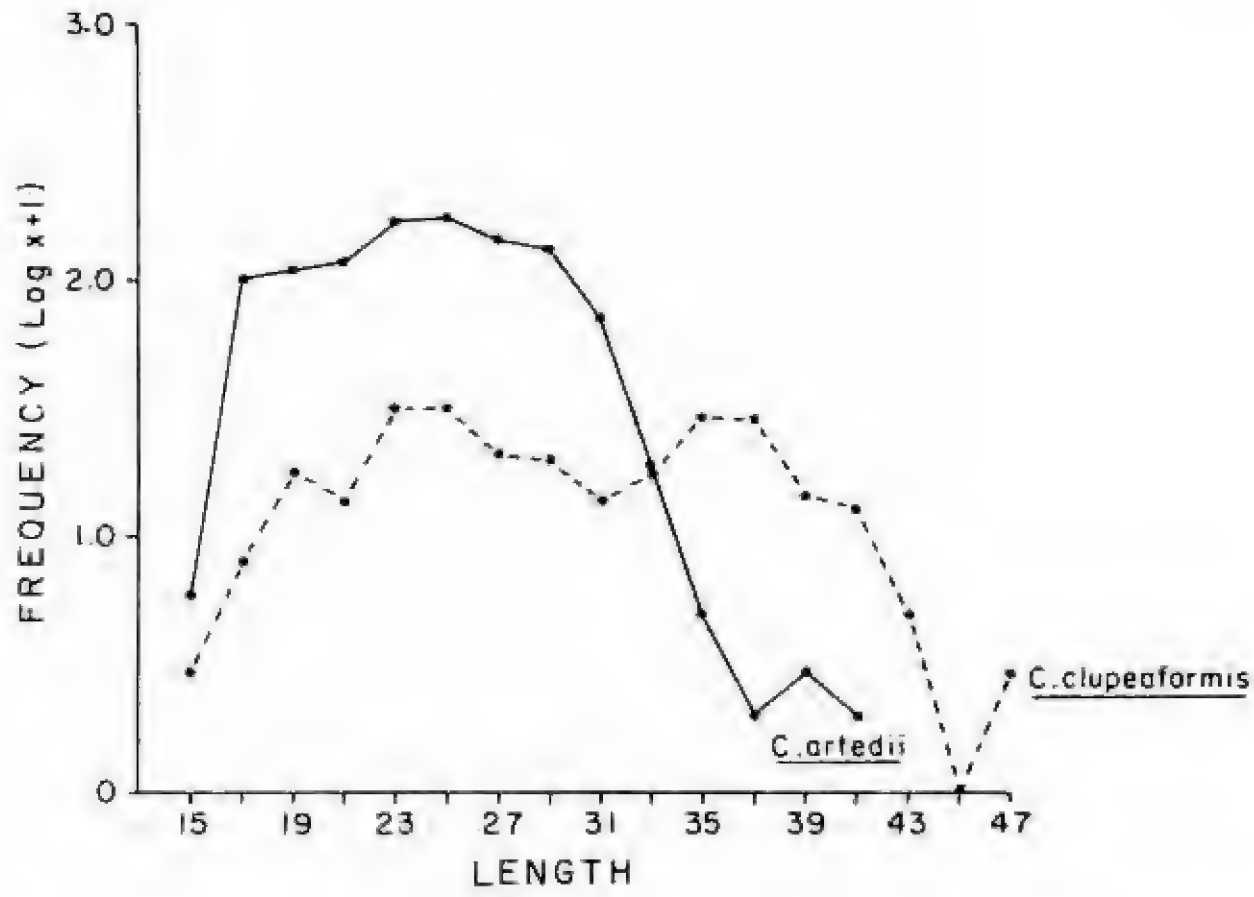

Figure 5

Logarithms of numbers (x) of cisco (solid line) and whitefish (dashed line) occurring in successive 2 cm length classes in all gill net samples from the Eastmain River and adjacent waters, 1980. Ascending left limb of curves represent length classes incompletely sampled by gill nets.

The greater survival costs and greater reproductive effort exhibited by cisco relative to whitefish suggest that selection should favor minimizing the costs of cisco migration by increasing the energetic efficiency of migration. Evidence in support of this hypothesis is provided by the observation that the somatic cost of migration is proportionately smaller for cisco than it is for whitefish, representing 28% of the somatic investment of reproductive cisco prior to migration compared to 35% in the case of whitefish (M_E , Table 2). However, the analysis of the efficiency of cisco's

upstream migration reveals behavior that does not appear to minimize energy expenditures. Gill net catches in the upstream section of the estuarine portion of the river revealed a series of peaks in cisco catches (Fig 6) that possibly represented the movement of schools of fish upstream to the spawning grounds. The most important peak occurred on August 4 at the downstream station (C2) and appeared 5 days later at the base of the first rapids, representing an average rate of displacement of 7.2 cm $\cdot s^{-1}$ (relative to the water). Extrapolating for the first 27 km of river, cisco take approximately 14 days to cover the estuarine section of the river. The analysis of 41 h of sonic tracking of one cisco revealed much meandering and retrograde motion. Observed swimming speeds were highly variable (mean = 11.42 cm $\cdot s^{-1}$, s.d. = 9.3, n = 84) and were not correlated with current speed. No upstream bias in orientation or swimming speed was observed. The remaining 4 cisco exhibited no displacement.

Cisco's average rate of upstream displacement does not account for the weight loss experienced by migrants in the estuarine portion of the river. Cisco swimming upstream at 7.2 cm $\cdot s^{-1}$ would expend approximately 4 g of lipid, whereas observed net weight loss is estimated to be equivalent to approximately 13 g of lipid in the estuarine portion of the river. This suggests that cisco swim at higher speeds than those revealed by sonic tracking and meander extensively. The apparent absence of a well-defined upstream bias in orientation is very costly for cisco. According to the model of Trump and Leggett (1980), cisco could minimize energy expenditures per unit distance by swimming upstream at a speed of 32 cm $\cdot s^{-1}$ (approximately 1 body length per second, 1 L $\cdot s^{-1}$). Such behavior would result in the loss of less than 1 g of lipid to complete the estuarine portion of the migration.

Despite the fact that cisco do not spawn until the beginning of November, gill net catches reveal that these fish have finished the estuarine part of their migration in early September (Fig 6), and wait at least 2 months before spawning, remaining on the spawning grounds without feeding. Furthermore, migrating in July and August at water temperatures of 15 to 20°C increases the cost of migration by 60% relative to a hypothetical migration in September at 10°C.

The upstream migration of whitefish appears even more meandering than that of cisco. Gill netting in the upstream section of the estuarine portion of the river (Fig 7) revealed an average rate of displacement relative to the water of 5.8 cm $\cdot s^{-1}$, only 0.8 cm $\cdot s^{-1}$ faster than the residual current. Extrapolating for the first 27 km of the river, whitefish take 38 days to cover the estuarine portion of the river. The analysis of 182 hours of sonic tracking of 6 whitefish revealed extensive meandering and retrograde motion. Observed swimming speeds were highly variable (mean = 10.98 cm$\cdot s^{-1}$, s.d. = 8.15, n = 159) and were not correlated with current speed. No upstream bias in orientation or swimming speed was observed. As 54% of the whitefish captured at the first rapids exhibited full stomachs, the application of the Trump and Leggett model is inappropriate. The meandering nature of the whitefish migration may be due in part to feeding (primarily on benthic organisms). Such feeding, however, does not appear to reduce the cost of the migration in terms of weight loss, relative to cisco (Table 2).

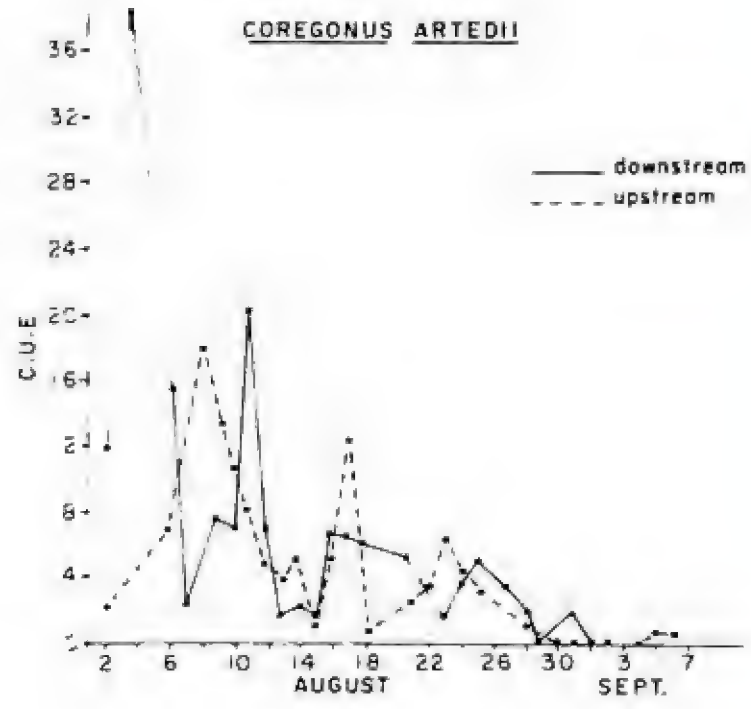

Figure 6

Catch per unit effort (C.U.E., numbers of fish per 24 h) by date of capture of reproductive cisco sampled by gill nets at station C2 (downstream, solid line) and station RB (upstream, dashed line), Eastmain River, 1983.

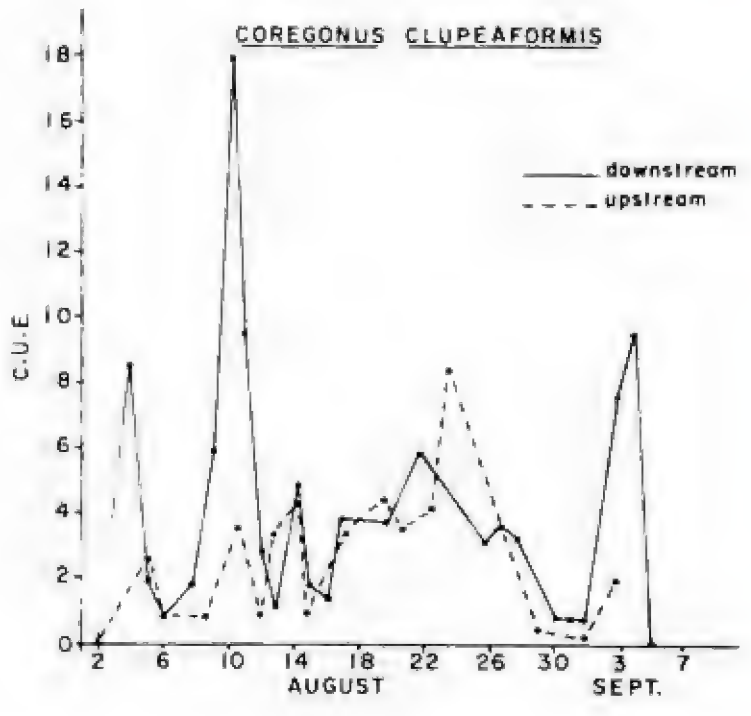

Figure 7

Catch per unit effort (C.U.E., numbers of fish per 24 h) by date of capture of reproductive whitefish sampled by gill nets at station C2 (downstream, solid line) and station RB (upstream, dashed line), Eastmain River, 1983.

The evaluation of the migratory efficiency of cisco has revealed 3 factors that contribute to augmenting energy expenditures during the reproductive migration: (1) the premature upstream migration at elevated water temperatures, (2) extensive meandering in the estuarine portion of the river, and (3) a wait of approximately 2−3 months (without feeding) in the vicinity of the spawning grounds prior to spawning. The early migration of cisco may be due to an environmental constraint other than spawning date. Wardle (1981) has demonstrated that contraction-time characteristics of swimming muscle determine maximum swimming speed and depend on fish length and ambient temperatures. Current measurements taken in the rapids in the fall of 1982 indicate that the fastest rapid exhibits an average speed of 1.5 m $\cdot s^{-1} \pm 0.02$. As this estimate is based on drogue experiments, it probably underestimates the speed at which a fish must swim to traverse the rapid. The maximum theoretical swimming speeds of fish as a function of length and temperature (Fig 8, first panel) calculated according to Wardle (1981) reveal that a standard cisco of 29 cm must traverse the rapids before water temperatures decline to approximately 7°C. This represents a minimum temperature as current speed is most probably underevaluated, and maximum theoretical swimming speeds overevaluate swimming ability as they ignore the problem of drag. Furthermore, such swimming speeds could only be maintained for several seconds and thus do not take into account the length of the rapids and the problem of swimming duration. Considering the average water temperatures in the Eastmain River between 1979 and 1982 (Fig 8, second panel), the month of September is characterized by a sudden decline in temperature such that the river reaches the critical 7°C level by the end of the month. Therefore we hypothesize that the early migration of cisco may be an adaptation to traverse rapid water downstream of spawning grounds before water temperature declines to critical levels.

The interaction of cold temperatures and maximum swimming speed does not appear to represent a constraint to the migration of whitefish. Referring to Figure 8, a whitefish of 36 cm can theoretically traverse the rapids at temperatures as low as 3°C, a temperature at which whitefish have already started spawning. Accordingly, gill net catches reveal that reproductive whitefish were captured 8 km downstream of the rapids in early September (Fig 7) suggesting that they continue to traverse the rapids throughout September for spawning in October. However, early migrating whitefish traversing the rapids in early August (Fig 7) must wait, without feeding, approximately 2 months in the vicinity of the spawning grounds prior to spawning. Temperature constraints to maximum swimming speeds cannot account for this observation.

The apparently non-optimal behavior exhibited by cisco in the estuarine portion of the river may be partially due to error in experimental procedures. The behavior exhibited by sonic-tracked cisco may largely be an artifact of the stress of handling and sonic tagging at elevated water temperatures. However, the results of netting studies (Fig 6) revealed a low net rate of displacement and also suggested poor

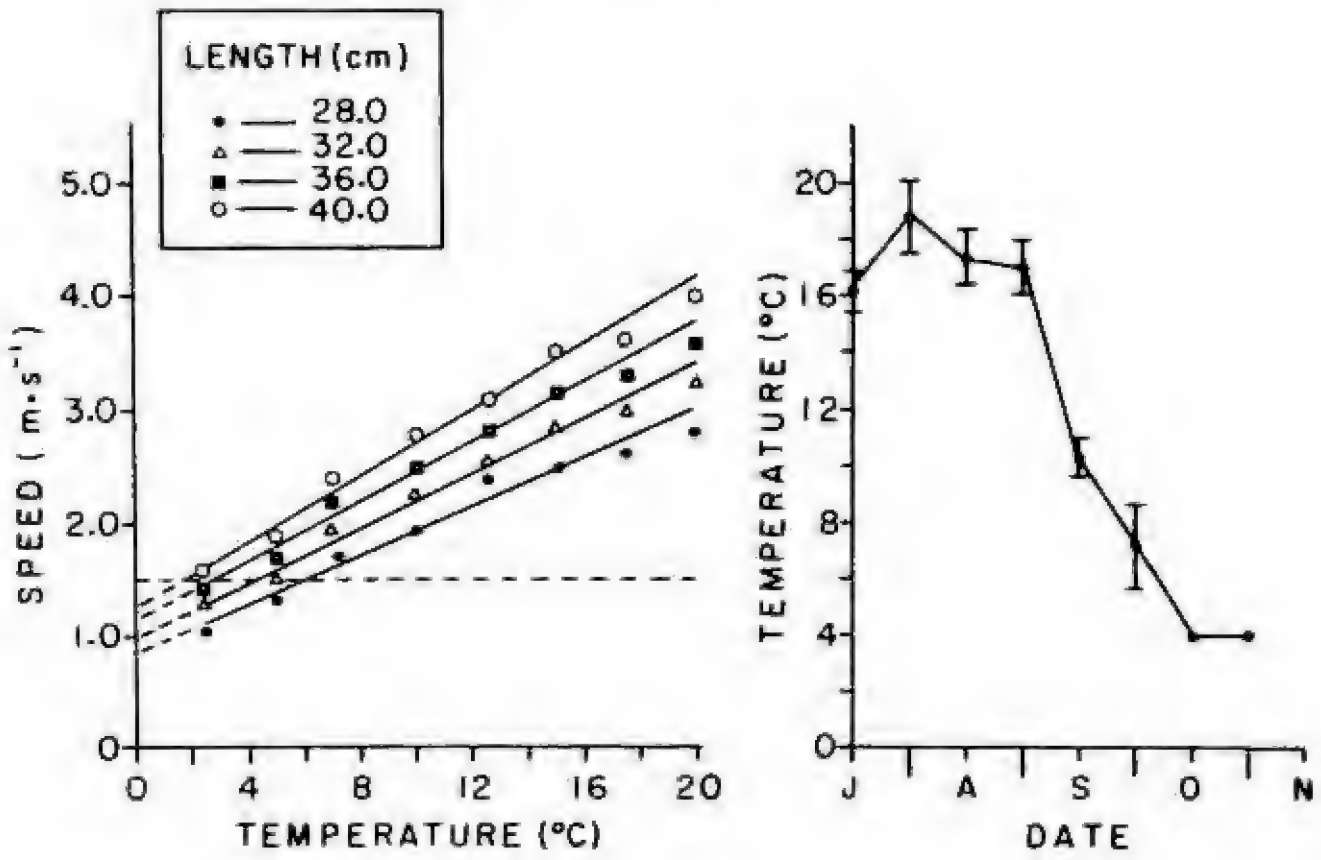

Figure 8

Left panel: Theoretical maximum swimming speeds as a function of temperature and body length calculated according to Wardle (1981). Dashed line indicates mean speed of fastest rapid, Eastmain River. *Right panel:* Mean water temperatures by month of the estuarine portion of the Eastmain River, 1979–1982. Vertical bars indicate standard deviations.

directional bias. The use of the constant b, calculated for rainbow trout, to estimate the optimal swimming speed of cisco may be a major source of error, although such interspecific extrapolation appears to be common practice (e.g., Trump and Leggett 1980). We are presently quantifying the constant b for both cisco and whitefish. However, both Weihs (1974) and Ware (1978) have noted that swimming speeds of 1 to 2 $L \cdot s^{-1}$ appear ideal for cruising and foraging over a variety of conditions and species. In the case of cisco, extensive meandering negates any advantage that may be provided by swimming at optimal speeds and we conclude that our evidence does not support the hypothesis that cisco are behaving so as to minimize energy expenditures per unit distance of migration.

The meandering and early upstream migrations of cisco and whitefish do not conform to optimality models of migratory behavior (Trump and Leggett 1980, Weihs 1984). Cisco swimming upstream at average speeds of 1 $L \cdot s^{-1}$ would traverse the estuarine portion of the river in 24 hours. Thus, cisco could theoretically remain on the feeding grounds in James Bay until the end of August and succeed in traversing the rapids before temperatures decline to critical levels at the end of September. In the case of whitefish, the meandering migration may be related to feeding, although early migrants must also bear the cost of waiting on the spawning grounds rather than exploiting feeding grounds in the bay or in the estuarine portion of the river.

We may at present only speculate about what factors are responsible for such prolonged and meandering migrations. The early migration of both species relative to spawning date may be due to physiological constraints that require these fish to enter the river when water temperatures are maximal. For example, Power (1981) hypothesized that sea and river temperatures in Ungava Bay, situated at the northern tip of Quebec, confine the migrations of Atlantic salmon *(Salmo salar)* to a very short period of time. Adult salmon arrive in the estuaries of their spawning rivers in mid-summer as suitable temperatures are attained in Ungava Bay (> 3°C). About 85% of the males have immature gonads when they arrive. Although mature fish spawn in the fall when they enter the rivers, the majority of males remain in fresh water over 12 months before their gonads ripen due to the short period of time during which river temperatures are suitable for maturation. In the case of the James Bay coregonines, sexual maturation of cisco and early migrating whitefish occurs mainly during upstream migration (Lambert and Dodson 1982b). In the case of females, vitellogenesis probably occurs in fresh water in the 2 months which precede spawning. Baggerman (1981) has reported that the time taken to attain sexual maturity in the stickleback *(Gasterosteus aculeatus)* is 2.5 times longer at 9°C than at 20°C indicating that vitellogenesis and subsequent ovulation develop much faster at higher temperatures. Thus the early migration of the coregonines, when river temperatures are maximum and exceed James Bay temperatures by 5°C to 10°C, may be an adaptation to insure completion of the maturation cycle for fall spawning.

In conclusion, the migration of both species is very costly, and although the somatic cost of migration is proportionately smaller for cisco than it is for whitefish, our evidence to date does not support the hypothesis that cisco are minimizing the cost of migration such that energy savings could be invested in either reproduction or survival. Although environmental constraints such as temperature and current speed may contribute to long periods of river residence away from feeding grounds, the extensive and energetically costly meandering exhibited by both species cannot at present be reconciled with the concept of energy conservation.

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OCEANIC MIGRATIONS OF ATLANTIC EELS (*ANGUILLA* spp.): ADULTS AND THEIR OFFSPRING

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ABSTRACT

Catches of variously sized American and European eel (***Anguilla rostrata*** and ***A. anguilla***) larvae (leptocephali) in the North Atlantic Ocean during the first 25 years of this century were used to infer that adults of these two catadromous species migrate to the Sargasso Sea, spawn and die, and that the offspring drifted on ocean currents to repopulate fresh waters of North America and Europe. Little additional work on oceanic migration of adults or leptocephali has been done until recently.

Routes and mechanisms of migration of adults are still unknown. However, a general compass-directional heading for each species and only a modest degree of precision of orientation may be sufficient for eels to reach the Sargasso Sea from most of their continental range. Tracking of eels (on the continental shelf) suggests that eels may have a compass mechanism of some type. Indirect evidence, from changes in countershading and morphological and physiological changes in the eye and swimbladder at metamorphosis to migratory adult, supports the hypothesis that the adults migrate in the upper few hundred meters of the ocean.

The persistent frontal zone meandering east-west across the Sargasso Sea at about 24–29°N may form the northern limit of spawning. Preliminary evidence from leptocephalus distribution on two transects across the front and from historical data supports this view. Some feature of the near-surface water south of the front or of the partially mixed waters of the front itself, perhaps odor or temperature, is probably the cue which triggers the cessation of migration by the adults.

Simulated drift on surface currents of leptocephali of the American eel from the spawning area suggests that the leptocephali move slowly northwest and accumulate northeast of the Bahamas. The accumulation persists for several months and leptocephali are only gradually introduced into the Gulf Stream system north of the Bahamas. These predictions are consistent with recent physical-oceanographic studies of the area and with collections of older leptocephali made in the Gulf Stream system.

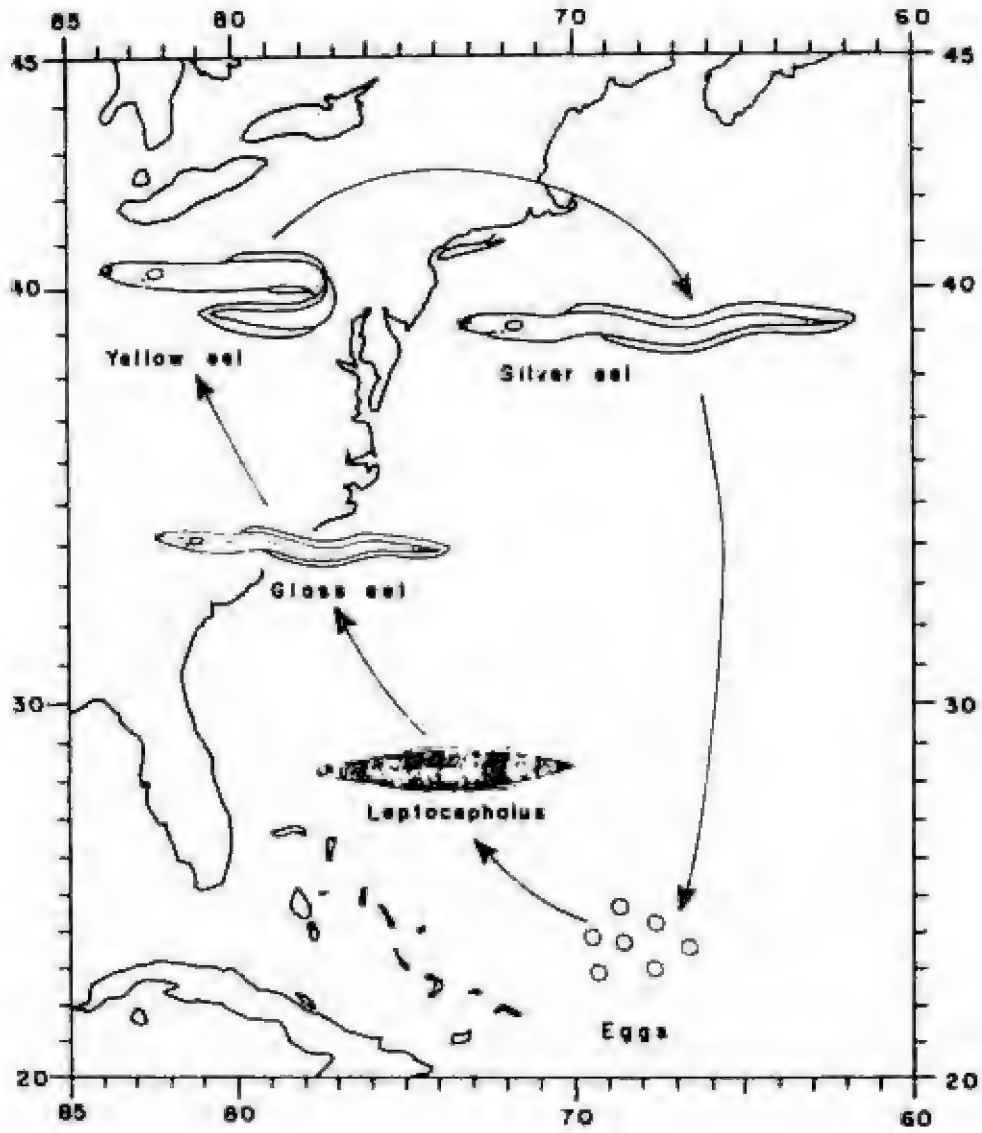

Figure 1
Catadromous life cycle of the American eel.

INTRODUCTION

When the Danish biologist Johannes Schmidt aboard the research vessel THOR captured a 7.5 cm leptocephalus of the European eel (***Anguilla anguilla***) west of the Faroes in May 1904 (Schmidt 1912), the chase was on. Prior to that time eel larvae had only been captured in the Mediterranean Sea, where spawning was assumed to occur. Over the next 25 years Schmidt accumulated collection records of over 10,000 European eel larvae and about 2,400 American eel (*A. **rostrata***) larvae. From the distribution of the smallest larvae Schmidt reached the conclusion that the European eel spawns in, and only in, the Sargasso Sea in the southwestern portion of the North Atlantic Ocean (Schmidt 1922). He also concluded that the American eel spawned in an overlapping area to the west, but he had records of only 22 larvae $\leq$ 10 mm long.

Despite the limitations of his data, Schmidt's conclusions about the life history were essentially correct—here depicted for the American eel (Fig 1). Leptocephali hatch from eggs spawned in the Sargasso Sea. They drift on ocean currents for nearly a year, metamorphose into glass eels which enter brackish or freshwaters from the Gulf of Mexico to Labrador. After several years as nonmigratory yellow eels, a second less dramatic but equally significant metamorphosis occurs. The resulting

silver eels migrate back to the Sargasso Sea to spawn and presumably die. European eels, distributed from Iceland to north Africa have a similar life cycle, but with a larval phase lasting two to three years.

Schmidt's conclusions about the oceanic life history of eels were inferred from the distribution in space and time of larvae of various sizes. He never captured adult eels in the open ocean, and he could not identify eel eggs in his plankton samples. Yet he stated his case so forcefully (e.g., Schmidt 1925) that his ideas have been generally accepted. Little additional work has been done on the oceanic migration and spawning of either species until recent years.

Now an appropriately Danish-led team is re-examining Schmidt's published and unpublished data (Boëtius and Harding, in press), and West German (Tesch 1982) and American (Kleckner, McCleave and Wippelhauser 1983) teams have active field-oriented research programs focusing on migration and spawning. The chase is on again! We now have the advantage of modern physical-oceanographic knowledge. However, much of what we know today is still inferred from indirect evidence, because despite a large German effort in 1979, adult eels still have not been captured in the open ocean—enroute to or in the Sargasso Sea. Furthermore, eel eggs still have not been identified in plankton samples from the Sargasso.

Bearing this in mind our paper speculates firstly on mechanisms of migration of adult eels (not so much the guiding "clues" (Harden Jones 1984), but rather ideas on some general mechanisms that might stimulate further work), secondly on what causes cessation of migration (a triggering "cue," Harden Jones 1984) and thirdly on mechanisms of larval migration. We treat only the oceanic migration of eels. Some pieces of the puzzle are fitted with the aid of data from the European eel, some with data from the American eel, some luckily with data from both. However, we think it safe to assume that the behavior of an eel from Bangor, Maine, is similar to that of an eel from Bangor, Wales.

MECHANISMS OF MIGRATION IN ADULT EELS

We offer three hypotheses concerning silver eel migration in the open sea:

Firstly, swimming in one general compass direction for each species, coupled with the inescapable oceanic circulation, is sufficient to allow eels to reach the spawning area from most of the continental range. The essential point is that it is not necessary to postulate that eels from Georgia, New York, and Nova Scotia must all swim in different directions. A southerly direction seems appropriate for American eels and perhaps a southwesterly direction for European eels.

Secondly, only a moderate directional orientation is sufficient to result in a successful migration. Here we heed the advice of Leggett (1984), who suggests that, "...progress of research on fish migration has been impeded by an excessive fixation on the concept of precision of oriented movement by individual fish..." The eel migration over thousands of kilometers is certainly spectacular, but it can probably be accomplished with a less than spectacular means of orientation.

Thirdly, migration occurs near the surface, at least in the upper few hundred meters, a point which might have significance with regard to mechanisms of migration.

The first two hypotheses are amenable to modeling as a cost-effective means of initial screening (DeAngelis and Yeh 1984, Neill 1984). To date we have constructed only a crude model. Our objective was to determine whether such a parsimonious mechanism could account for return of eels to the Sargasso Sea and to decide whether modeling is worthy of further effort. Nine preliminary track simulations were made as follows: an hypothetical American eel swam in each of three directions (SW, S, SE) from each of three locations covering much of their geographic range (Savannah, Georgia; Hudson River, New York; Cape Breton Island, eastern Nova Scotia). Starting dates were 15 September, 15 October, 15 November for the three locations, respectively. The animals swam at 40 $cm \cdot s^{-1}$ in the chosen heading. This speed is reasonable and conservative, based on our tracking experiments (J. McCleave, M. Greer Walker and G. Arnold, unpublished data), and in body lengths is approximately $1-1.2$ $L \cdot s^{-1}$ for an average silver male and $0.6-0.7$ $L \cdot s^{-1}$ for an average silver female. The conservative speed compensates for the fact that an absolute compass heading was assumed, rather than a more reasonable spread of headings which would lower the apparent speed. The choice of three headings is based on the assumption that any orientational ability would not be absolute.

Each simulated eel moved in a direction that was the resultant of its swimming vector and the surface water current vector as summarized by month or quarter for each 1° of latitude × 1° of longitude in published atlases. One constraint was placed on the resultant vector to simplify computation—the fish could move only from the center of one 1° cell to the center of one of the eight surrounding cells, i.e., the resultant vector directions were shifted to the nearest approximate cardinal or half-cardinal direction.

Only three of the nine simulated tracks actually entered the American eel spawning ground as delimited by the historical catches of larvae $\leq$ 7 mm long (Fig 2). However, four others came close enough to be assumed successful, when one considers the crudeness of the model and arbitrariness of the spawning ellipse. Dates of arrival or near arrival were before or during the spawning season. The southeasterly swimming eel from Cape Breton went too far east and was considered lost. The southwesterly swimming eel from Savannah got caught in a loop and was considered lost too.

There is no evidence to show that eels from North America do swim south. We present these simulations merely to show that mean headings anywhere within a 90° compass sector are probably sufficient to bring eels to the spawning area from a good portion of the range—one that must encompass 90% of the potential spawners. We conclude that the modeling warrants further development.

Given reasonable encouragement from the model simulations, is there any evidence that adult eels can swim in a general heading in midwater? We offer a qualified "yes." Appropriate experiments have not yet been conducted off the continental shelf, but over several years we have tracked adult European eels in the

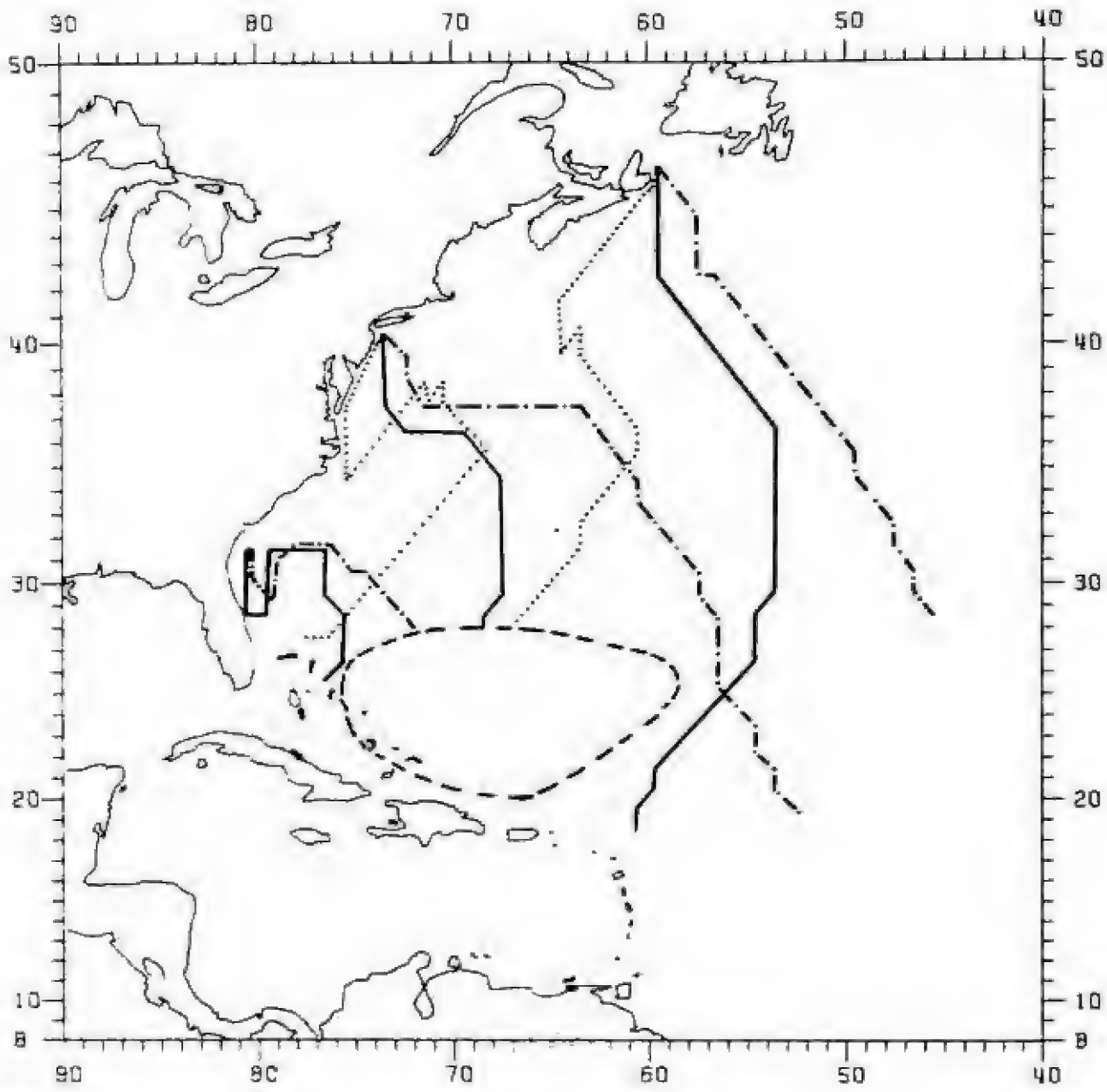

Figure 2

Simulated tracks of American eels swimming southwest, south and southeast from three locations. Presumed spawning area delimited by dotted line.

North Sea using the sector-scanning sonar of the Fisheries Laboratory, Lowestoft, England (J. McCleave, M. Greer Walker and G. Arnold, unpublished data). This technique, well described in the literature (e.g., Greer Walker, Harden Jones and Arnold 1978), allows determination of the depth of the fish and the depth of water below the fish in addition to location. Most tracking was conducted in an area of well-behaved bidirectional tides, and recording current meters were deployed at two depths and two locations in the tracking area. Thus we could interpolate the water currents to a particular depth. By vector subtraction of the water current from the over-ground movement of the eel, the direction of swimming through the water for each 15-min period could be determined.

A portion of one track of a 77-cm long yellow eel, i.e., an eel not yet in the migratory state, is illustrative. The over-ground track shows movement to the southwest in initial and final portions of the track with some apparent drifting with the tide in the middle of the track (Fig 3).

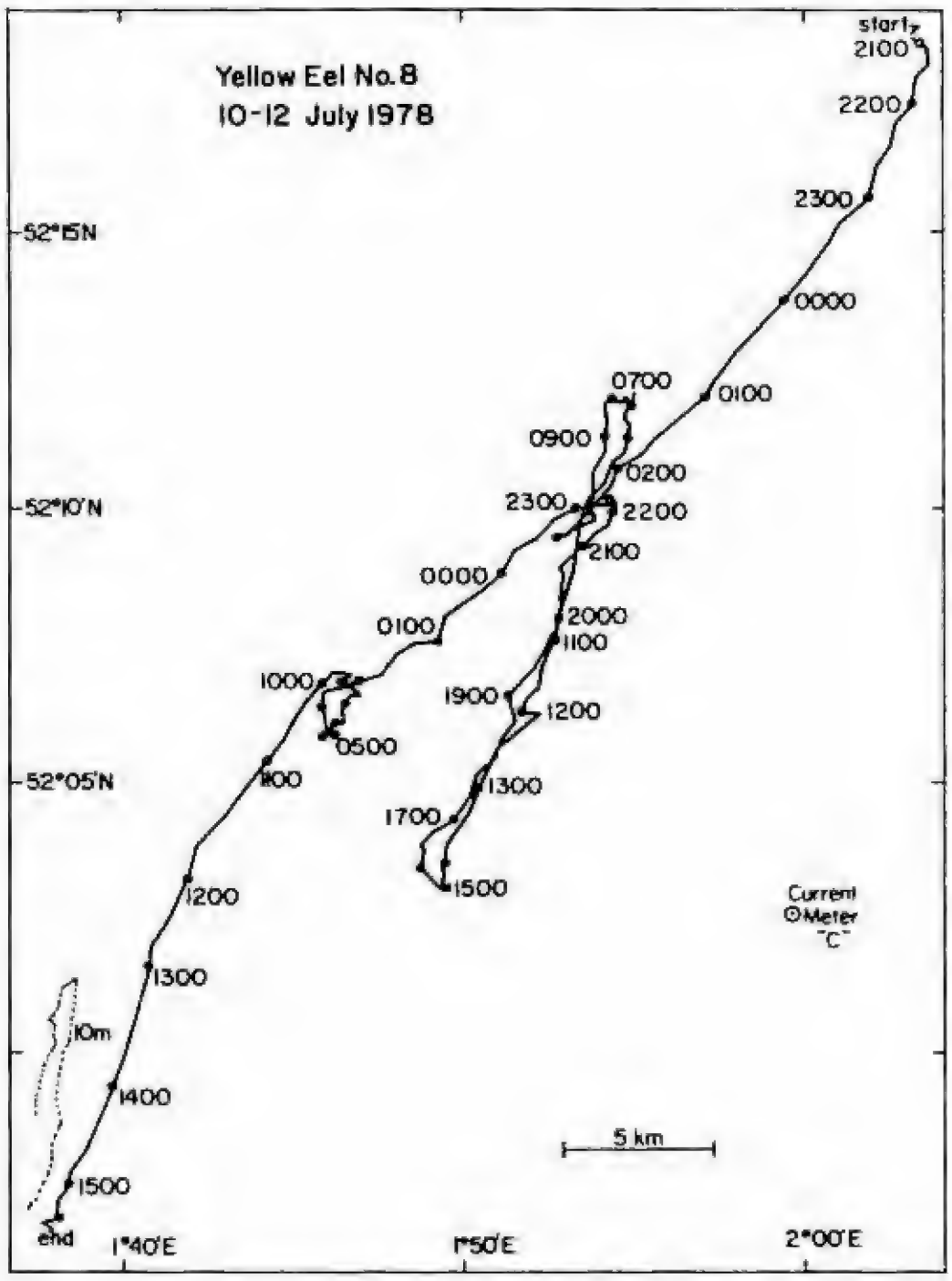

Figure 3

Track of a yellow-phase European eel in the North Sea off Lowestoft, England. Open circles = northerly flowing (flood) tides; closed circles = southerly flowing (ebb) tides. (J. McCleave, M. Greer Walker and G. Arnold, unpublished data.)

Progressive 15-min tracks of tidal movement, and over-ground and through-water eel movements, were calculated for the initial two tides (Fig 4). The first is a southerly flowing (ebb) tide at night and the second a northerly flowing (flood) tide during daytime. The circular diagrams show that the 15-min through-water headings during each of the two tides were tightly clustered. Except for a brief touchdown at the change of tides, the eel was in midwater. The average eel depth, based on 5-min observations, was < 13 m and < 5 m during the two tides over an average bottom depth of 32 m.

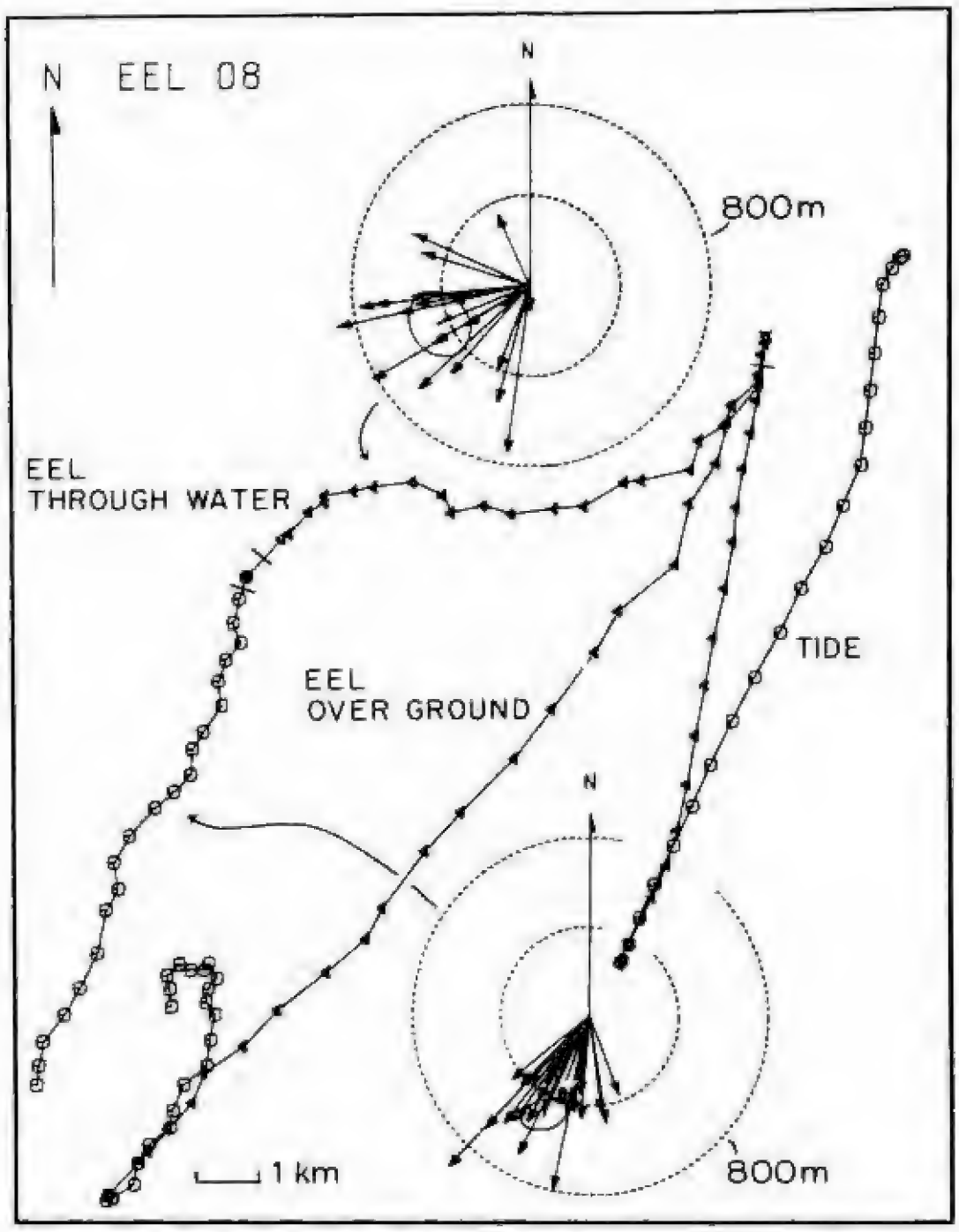

Figure 4

Progressive 15-min vectors of a yellow-phase European eel during first two tides of track shown in Figure 3. Through-water vectors obtained by vector subtraction of tidal vectors from over-ground vectors. Circular diagrams show individual 15-min through-water vectors and the mean vector with its 95% confidence ellipse for each tide. Circles = northerly tide; triangles = southerly tide; open symbols = day; closed symbols = night.

The tidal, over-ground and through-water vectors were then subjected to elliptical statistical analyses (Batschelet 1981). In essence, both direction ***and distance*** are used in a bivariate procedure. A mean vector and its 95% confidence ellipse are used to draw statistical inferences. For these two tides, because the 95% confidence ellipse for through-water vectors does not include the origin, there was significant through-water swimming (Fig 5). In the second tide the over-ground ellipse includes the origin, which indicates that the eel did not move a significant distance over the ground. This station-keeping was accomplished by swimming through the water against the tide.

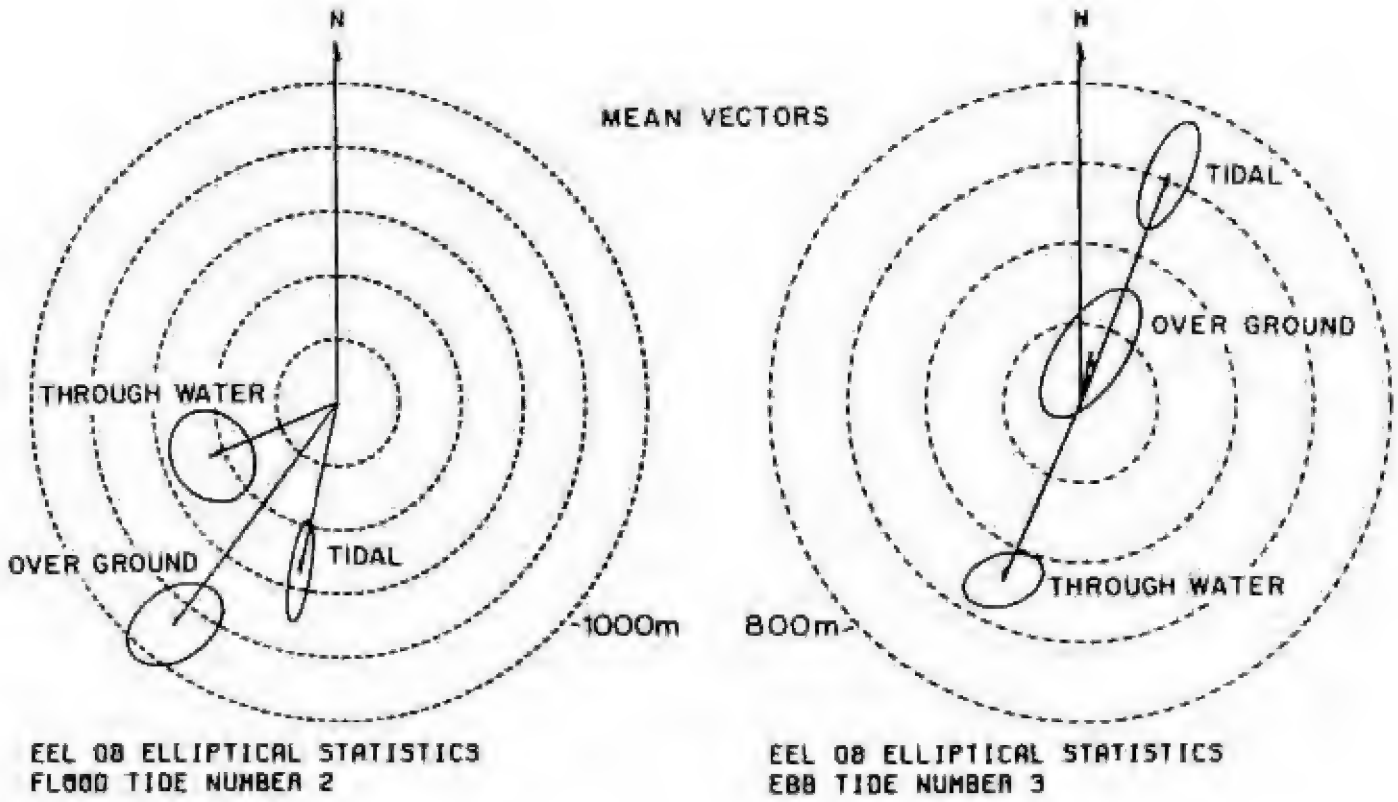

Figure 5

Mean vectors and 95% confidence ellipses for 15-min over-ground, tidal and through-water vectors of portion of track of a yellow-phase European eel shown in Figure 4. Confidence ellipses not encompassing the origin indicate statistically significant vectors.

Leggett (1984) has warned against concentrating on fish that behave in a particular, well-oriented manner, but we point out that nearly all of the 15 eels we have tracked had periods of oriented swimming in midwater. These tracks are admittedly a far cry from thousand-kilometer swims, but they are essentially the only available data. Tesch's (1978a, b) tracks at the edge of the continental shelf, especially in the Bay of Biscay, are not instructive in this regard because he does not show the actual tracks in most cases, the inaccuracy of Decca positions is mentioned but not evaluated, and the water currents are unknown.

With regard to the third hypothesis, what evidence is there for a near-surface migration? Despite a nagging photo taken by Robins, Cohen and Robins (1979) of one (or possibly two) adult-sized eels swimming just above the bottom at 2000 m in Tongue of the Ocean in the Bahamas, all other evidence points to migration in the upper few hundred meters. Tesch (1978a, b) tracked three silver eels fitted with depth-sensitive transmitters on the European continental slope. Over about 2000 m of water the three eels mostly swam at depths between 50 and 400 m, but tracks were short and terminated due to pressure-transmitter failure. All of those who have tracked eels with equipment that can discriminate depth of swimming (Stasko and Rommel 1974; Tesch 1978a, b; Westerberg 1984; J. McCleave, M. Greer Walker and G. Arnold, unpublished data) have observed frequent, substantial vertical movement, but have also observed long periods of movement near the surface during both day and

night. However, none of these reports is of truly oceanic eels in a truly oceanic situation.

The *indirect* evidence for a meso- or epipelagic migration is more compelling than the direct evidence:

1. Metamorphosis from yellow to silver eel implies a color change. Indeed silver eels are dramatically darker dorsally and whiter ventrally than yellow eels due largely to rearrangement of purines in the integument (Pankhurst and Lythgoe 1982). The color change is evident before migration to sea and is maintained through sexual maturation of hormone-injected eels. Such countershading is only useful in the photic zone of the ocean—the upper 1000 m for certain, probably the upper 600 m. Most mesopelagic fishes found below 600 m during the daytime are dark colored and not countershaded (Marshall 1971, 1972).
2. Metamorphosis to silver eel involves substantial changes in the visual system morphology and biochemistry. Eye diameter of both species increases by a factor of 1.5 (Boëtius and Boëtius 1967, 1980; Winn, Richkus and Winn 1975). Concomitant morphological changes at least in the European eel include proportional increase in lens diameter, increase in retinal surface area, addition of new rod cells to maintain density, increase in convergence of rods on each neural pathway, and decrease in cone density (Pankhurst 1982, Pankhurst and Lythgoe 1983). Visual pigments change during metamorphosis to a mixture of two rhodopsins with wavelengths of maximal absorption of 482 nm and 501 nm, with the 482-nm variety predominating (Beatty 1975). These morphological and biochemical changes largely occur prior to migration and adapt the eel for vision in dim, monochromatic, blue light. Such photic conditions are found in the mesopelagic zone of clear oceanic waters by day (Jerlov 1976) and in the epipelagic zone by night.
3. Morphological changes also occur in the swimbladder during metamorphosis which allow silver eels to maintain an inflated swimbladder at greater depth than yellow eels, but probably not much deeper than 150 m (Kleckner 1980a). Maintenance of a gas-filled swimbladder depends upon the rates of gas deposition via the rete mirabile and of gas loss by diffusion through the swimbladder wall. Both rates are hydrostatic-pressure dependent. Retial capillary lengths increase about 2.5 times (Kleckner and Krueger 1981) and are comparable in length to other fishes which inhabit the upper mesopelagic zone. Guanine content of the swimbladder wall increases to reduce diffusive losses (Kleckner 1980b). Thus the swimbladder data argue for an upper mesopelagic or epipelagic migration.

Speculation on guidance mechanisms for the adult migration are premature, but we offer three comments. Firstly, potential orientational features, such as direction-resolvable acceleration due to ocean swell (Cook 1984) or direction-resolvable Langmuir circulation due to wind (Barstow 1983, Leibovich 1983), that might give a general guidance if the swell or wind were of a prevailing nature are only useful to a fish in the upper pelagic zone. Secondly, any form of celestial orientation is also restricted roughly to the epipelagic zone, because the compression and distortion of

the aerial field of view by refraction through Snell's window and the shift with depth of the angle of maximum radiance toward the vertical (Jerlov 1976) make determination of sun or moon azimuth or altitude virtually impossible except near the surface. Thirdly, silver American eels have magnetic remanence in their heads (M.M. Walker, personal communication), which suggests that eels are likely to join the growing list of migratory vertebrates that have magnetite in their ethmoid regions.

TERMINATION OF SILVER EEL MIGRATION

By some set of clues eels ***are*** guided across the North Atlantic. But what cue triggers them to cease migrating and to spawn in a particular area when, especially in the case of the European eel, spawning seems to occur in a particularly restricted area in the middle of "apparent nowhere" over 5-km deep water?

We have hypothesized that adults of both species cease migrating when they encounter or cross from north to south an extended frontal zone which meanders east-west across the Sargasso Sea at about 24−29°N latitude (Kleckner et al. 1983, mentioned by Wegner 1982). Some feature of the surface waters south of the front or of the partially mixed waters of the front itself is probably the triggering cue. As a result the frontal zone is likely the northern limit of spawning, with spawning occurring in and to the south of the frontal zone.

This frontal zone, which is located within the North Atlantic Subtropical Convergence, is marked by abrupt horizontal temperature changes that allow its position to be determined from satellite infrared images (Fig 6). The front is persistent from year to year, at least during winter and spring (the important time for eel spawning), although its position varies annually, seasonally and even day to day as mesoscale eddies deform it into a sinuous pattern (Voorhis, Schroeder and Leetma 1976; Leetma and Voorhis 1978; Voorhis and Bruce 1982). The front separates a permanently stratified, warm, saline surface water mass in the southern Sargasso Sea from a cooler, less saline, seasonally stratified surface water mass in the northern Sargasso Sea (Fig 7) (Katz 1969, Voorhis 1969).

South of the front a permanent thermocline is located just above the boundary between common and warm, saline water masses. The temperature-salinity diagram has a characteristic signature (Fig 7, upper right). North of the front the temperature-salinity diagram has a quite distinct signature (Fig 7, upper left). Mixing does occur in the frontal zone and creates a layer with intermediate and distorted characteristics.

The essential points with respect to the migration hypothesis are that the front is distinct horizontally, is distinct vertically especially to the south and is a shallow water phenomenon.

Evidence from three sources—historical data, University of Maine research cruises in 1981 and 1983, and a West German research cruise in 1979—supports the hypothesis.

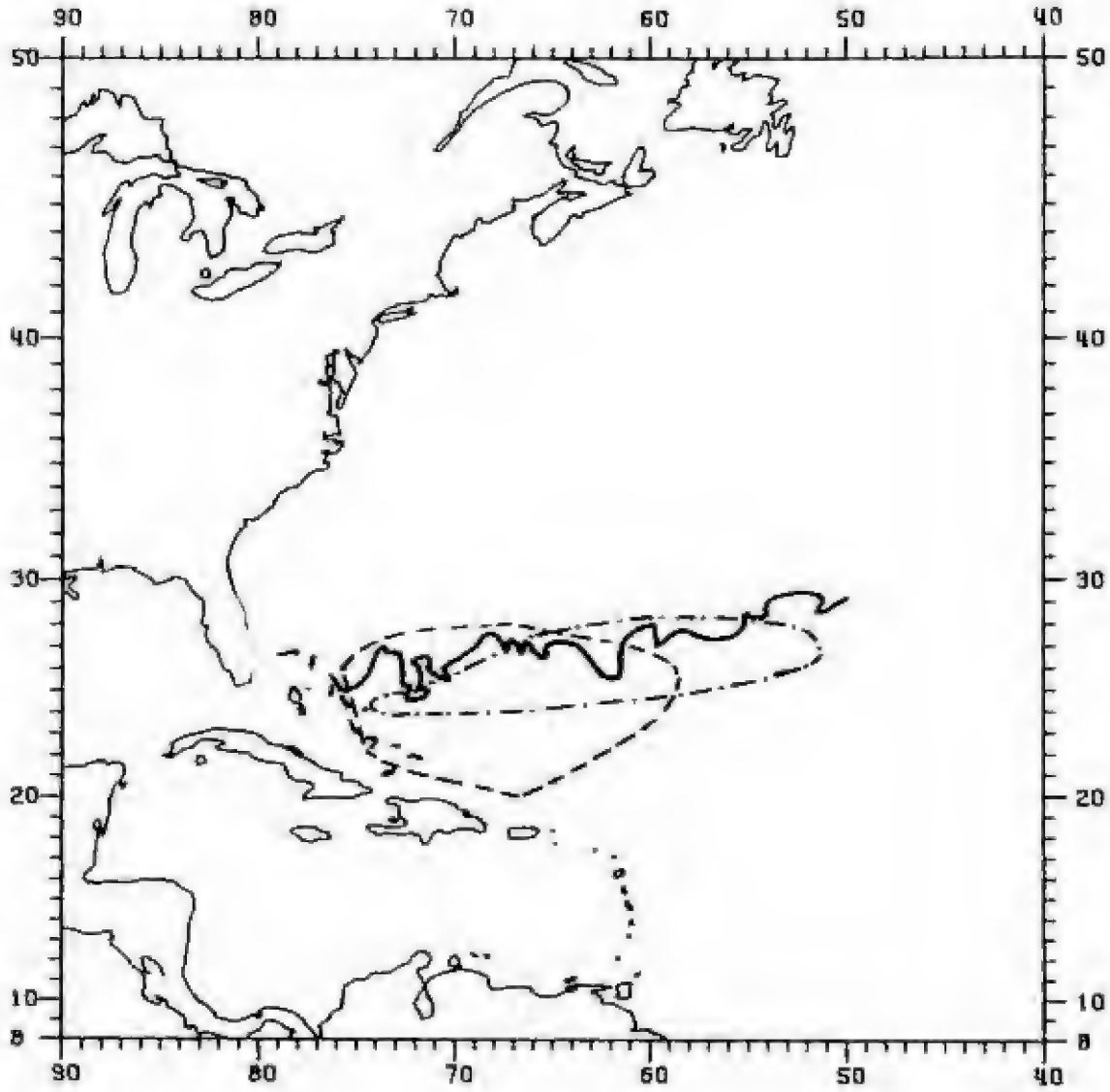

Figure 6

Frontal zone in the Sargasso Sea in early April 1983 as determined from satellite imagery (solid line) and areas of collection of American and European eel leptocephali ≤ 7 mm total length (dashed line and dashed/dotted line, respectively).

We have compiled all records of capture in the North Atlantic Ocean of small ***Anguilla*** leptocephali that we could unearth—including Schmidt's data, other published data, unpublished data from various collections we examined (Kleckner and McCleave, in press), the 1979 West German data (Schoth and Tesch 1982) and our 1981 data (Wippelhauser, McCleave and Kleckner, in press). All catches of American eel leptocephali ≤ 7 mm total length (188 specimens) were obtained within a broad ellipse extending eastward from the Bahamas to about 58°W longitude (Fig 6). All catches of European eel leptocephali ≤ 7 mm long (226 specimens) were obtained within a narrow, overlapping ellipse (Fig 6)—affectionately referred to as "Schmidt's cigar" by those of us working on the problem. Based upon assumed length at hatching and a growth curve developed from historical data, leptocephali ≤ 7 mm are ≤ 17 days old and would not have drifted far.

The coincidence between the northern limits of small American eel larvae and the frontal area, and between the long axis of "Schmidt's cigar" and the frontal area, is highly suggestive (Fig 6).

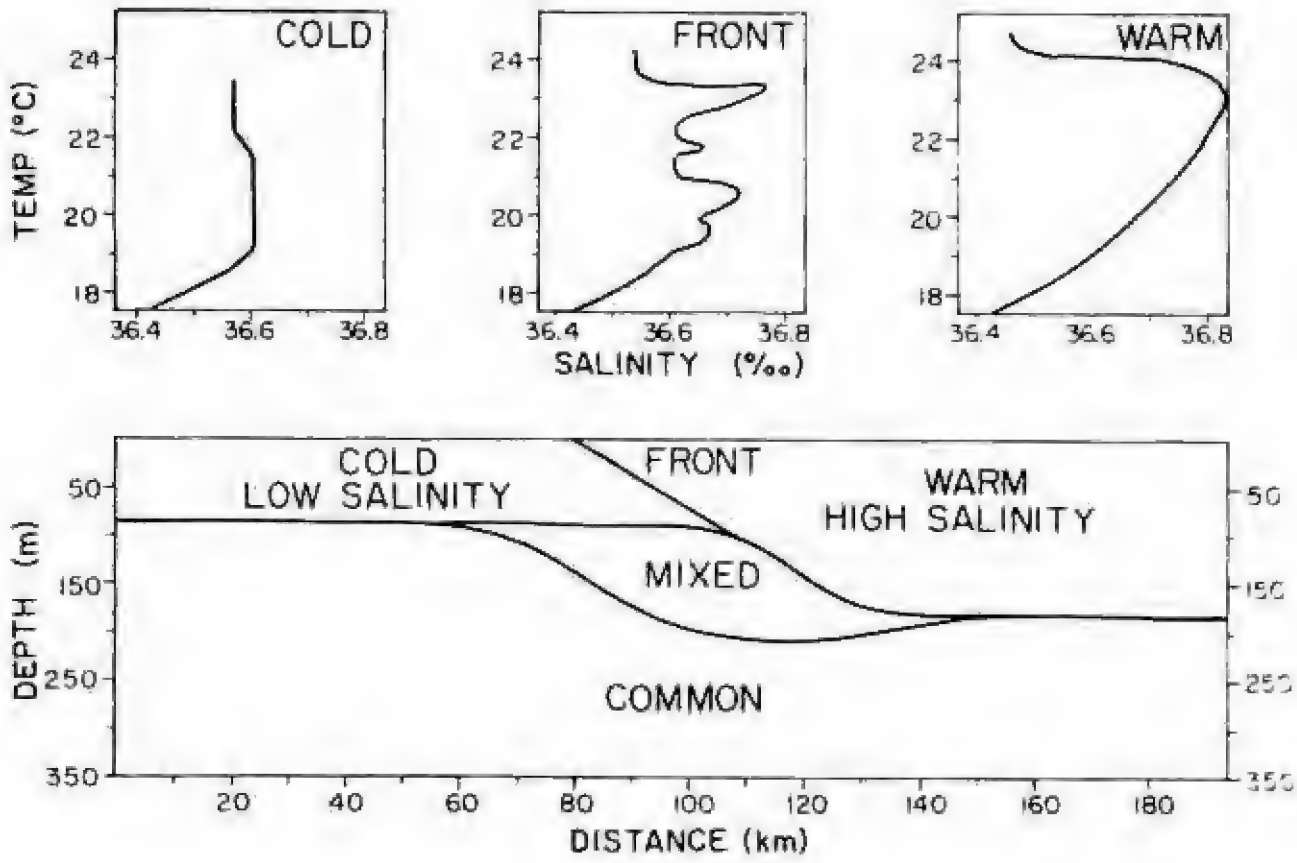

Figure 7

Schematic diagram of transect through frontal zone from north (left) to south (right) (lower panel) and the temperature-salinity correlation diagrams used to identify water masses (upper panels).

On a survey cruise in February 1981 aboard RV COLUMBUS ISELIN, one transect of stations was made which crossed from the cold side of the front to the warm side and which then grazed the cool water again (Kleckner et al. 1983). A 3-m Isaacs-Kidd midwater trawl fully lined with plankton netting was used in standardized oblique tows to sample for small leptocephali along the transect. Sample volumes were similar among tows.

At the cold water stations we caught 0 and 1 American eel leptocephalus (Fig 8). At the warm water stations we caught from 6–68 American eel leptocephali per tow, including specimens as small as 4 mm total length.

On the strength of the historical and survey data, two cruises were conducted aboard RV CAPE FLORIDA in February and April 1983 to examine the front hypothesis relative to the American eel and European eel, respectively. On each cruise two transects of stations were made across the frontal zone in different areas. Sorting of this material is not completed, but preliminary data are available from the second transect of the first cruise.

The front is identified from isopleths of water density—the result of consideration of both temperature and salinity data obtained by conductivity-temperature-depth casts at each station—along a north-south transect (Fig 9). Steep inclines of density isopleths are a better indication of the frontal zone than are isotherms.

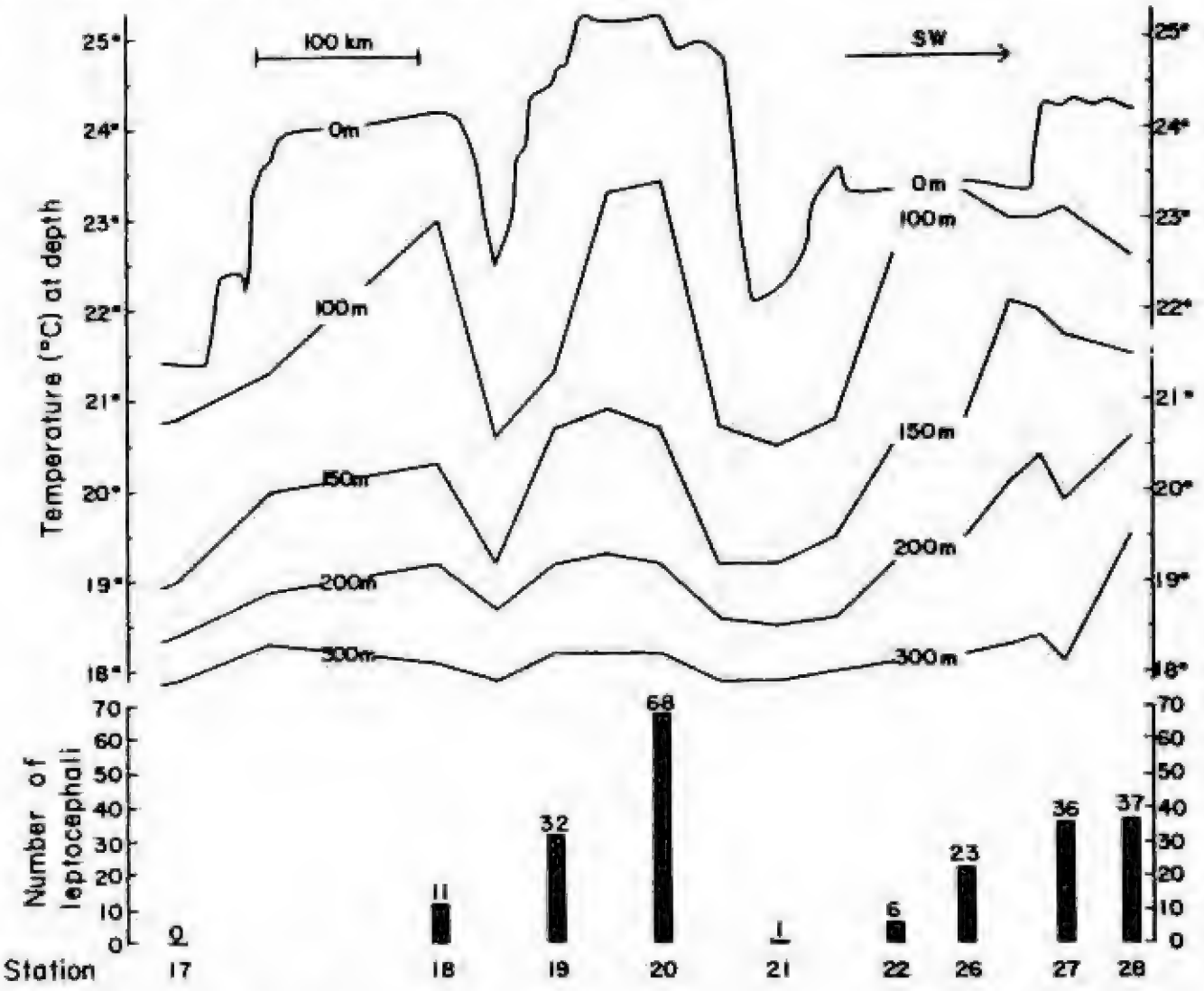

Figure 8

Temperatures at selected depths and numbers of American eel leptocephali caught in standardized trawls along the thermal front, 25–27 February 1981. Rapid vertical excursions in the temperature profiles indicate where the thermal front was crossed. Surface temperatures based on continuous recordings; subsurface temperatures based on expendable bathythermograph profiles. (From Kleckner et al. 1983.)

On the north side of the front no leptocephali were caught, but in and south of the frontal zone, 2–14 American eel leptocephali were caught per 10^5 m^3 of water strained (Fig 9). All larvae were ≤ 10 mm long, and most stations had larvae ≤ 5 mm long. This transect, as the 1981 transect, suffers from lack of more stations north of the front, because temperature data at sea suggested the northern edge of the front was farther south than it turned out to be when density was plotted. Also, the low absolute numbers of leptocephali caught suggests that the samples were taken before the peak of the spawning season. Nevertheless these preliminary data support the hypothesis, and the complete analysis of data from the two cruises should prove instructive.

Data on distribution of leptocephali of both species ≤ 10 mm long (Schoth and Tesch 1982) and on hydrography (Wegner 1982) from the 1979 West German cruise, although not specifically collected for the purpose of testing the hypothesis, do include data from partial or complete transects across the frontal zone. These data include numerous negative stations both north and south of the front and clearly show that small larvae of both species are found in the frontal region.

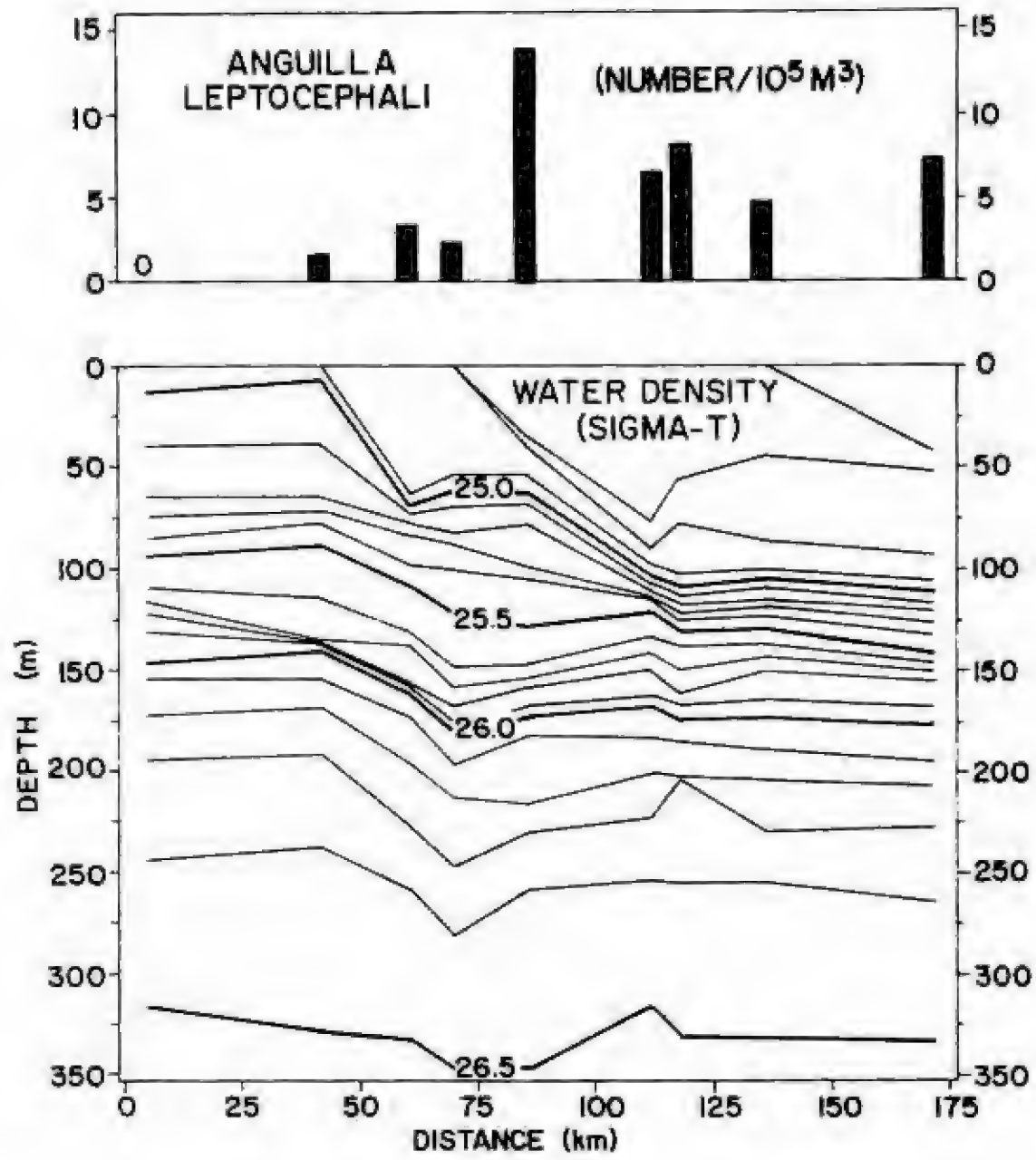

Figure 9

Isopleths of water density at depth and numbers of American eel leptocephali caught per 10^5 m^3 of water strained in standardized trawls across the frontal zone, 16–19 February 1983. Vertical excursions of the density isopleths indicate the front. Densities based on conductivity—temperature—depth profiles.

We have no evidence for what the triggering cue associated with the southern water mass is, but temperature and odor seem likely candidates. Measured horizontal temperature gradients in the frontal zone may sometimes be $2°C \cdot km^{-1}$ (Voorhis 1969). Several biological distinctions in the northern and southern water masses have also been reported in the literature. Species composition of phytoplankton, zooplankton and mesopelagic fishes all differ (Hulbert 1964; Colton, Smith and Jossi 1975; Backus, Craddock, Haedrich and Shores 1969). Radiolaria increase relative to Foraminifera (Cifelli and Sachs 1966).

Might not the southern Sargasso water mass be imbued with a bouquet to which the leptocephali imprint—a bouquet every bit as distinctive to a returning silver eel as that of home stream water to a returning silver salmon?

In either case it seems that the silver eels must migrate in, or at least frequently enter, the uppper 150–200 m of water as the two surface water masses are underlain by a common water mass. Perhaps it would be wise to consider Westerberg's (1984) point that movement vertically on a scale of a few tens of meters can often provide information on changes that occur horizontally only over scales of tens of kilometers. Thermal and odor gradients are far steeper vertically. Furthermore the odor gradient may be steepened even more as free amino acids—potent olfactory stimuli for many fishes—may accumulate in upper layers of pycnoclines (Liebezeit, Bolter, Brown and Dawson 1980).

In this light an upper mesopelagically migrating, vertically mobile silver eel now seems to make sense.

MECHANISMS OF MIGRATION OF LEPTOCEPHALI

Schmidt assumed that the leptocephali of both species drifted on surface currents to repopulate the rivers of North America and Europe. This seems a reasonable assumption given the general circulation pattern of the North Atlantic Ocean. However, a critical examination of the assumption has never been made, although Harden Jones (1968) discussed it in some detail. We are now carefully considering the role of passive drift in the migration of leptocephali, particularly those of the American eel. We are using three approaches aided by modern physical-oceanographic knowledge and computers—tools not available to Schmidt or even to Harden Jones.

As the first approach, Power (1984) developed a numerical simulation model of the drift of a planktonic organism in surface waters which was based on the advection-diffusion equation. Using this model Power and McCleave (1983) simulated drift of American eel leptocephali for the first 270 days of life from an assumed birth on 1 March. Surface water currents were calculated monthly for a 1° latitude × 1° longitude grid from raw ship's drift observations. Data for American eels (Kleckner and McCleave 1982) and for European eels (Schoth and Tesch 1982, 1983) show that leptocephali of both are found largely in the upper 300 m. Thus the model was developed using only the two horizontal dimensions. Because the leptocephali were assumed to maintain themselves in the surface waters, the equations were solved with no assumptions regarding fluid continuity. Leptocephali would thus be concentrated in regions of net water convergence, i.e., downwelling, and dispersed from regions of divergence, i.e., upwelling.

Drift simulations were started with point sources of "leptocephali" from the various locations in the presumed spawning area. The model calculated fluxes across all cell boundaries, and the output was concentration of leptocephali in each cell relative to the initial concentration. Concentrations were contoured in steps of one order of magnitude. The results (Power and McCleave 1983) are illustrated here with the simulated distribution of catches of small American eel leptocephali at 25°N, 69°W (Fig 10).

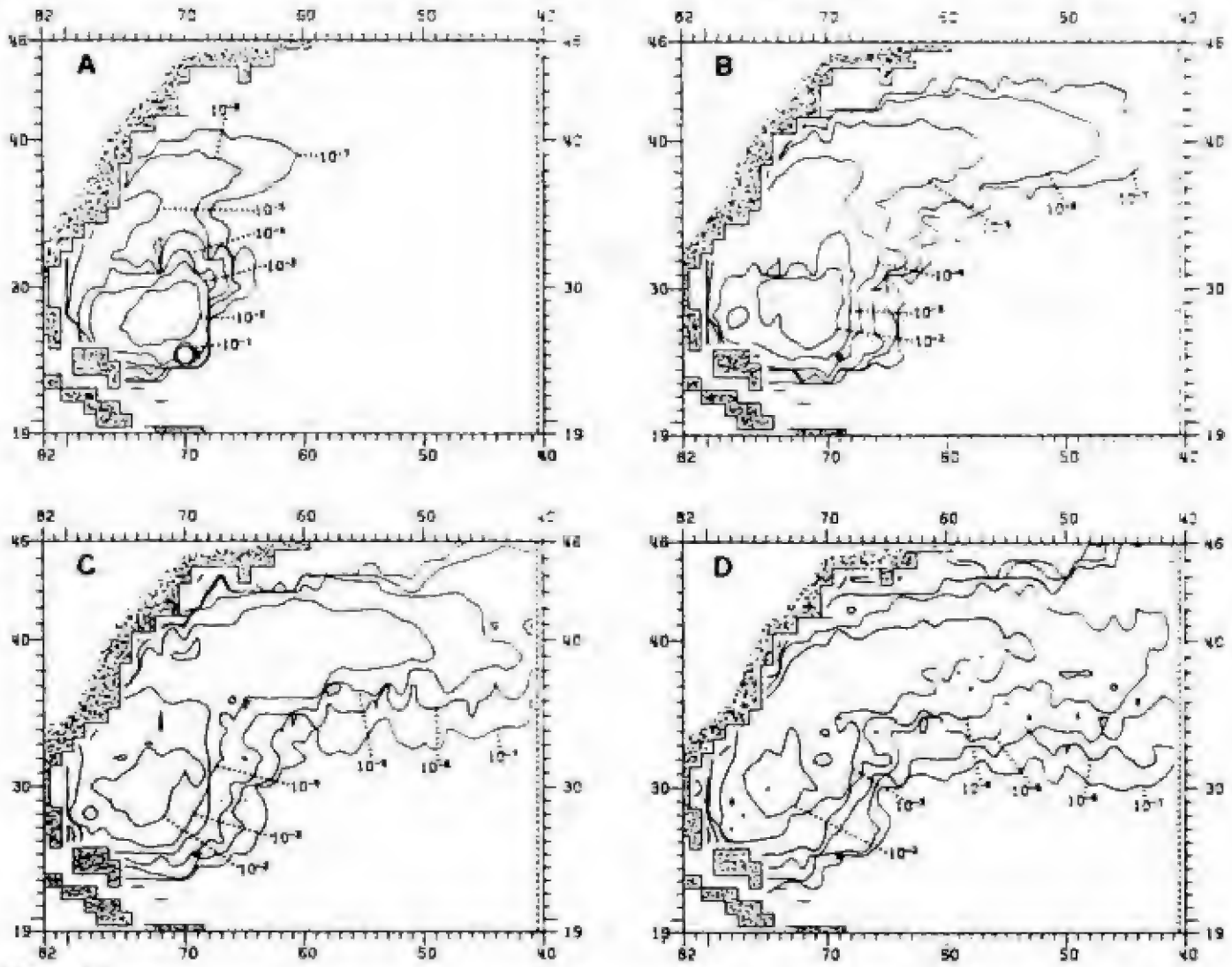

Figure 10

Concentration contours of American eel leptocephali after simulated drift for various periods from an assumed 1 March starting date and 25°N, 69°W starting location. (A) 90 days of drift (30 May). (B) 150 days of drift (29 July). (C) 210 days of drift (27 September). (D) 270 days of drift (26 November). Concentrations are expressed as a proportion of starting concentration. (After Power and McCleave 1983.)

After 90 days of drift (30 May) the major concentration of larvae had moved only slightly to the northwest (10^{-2} contour, Fig 10a). After 150 days (29 July) and 210 days (27 September) of drift the concentration had remained intact and moved only slightly more to the northwest (Fig 10b,c). Larvae were present in the Gulf Stream, but in relatively low concentration. Even after 270 days of drift (27 November) the concentration remained, but by then leptocephali were well distributed along the Gulf Stream (Fig 10d). The simulations were not carried beyond 270 days, as leptocephali of that age begin to metamorphose into glass eels (Kleckner and McCleave, in press), and the assumption of passive transport may no longer be valid. The pattern of movement was similar from the other starting points.

Two points emerge from these simulations, which we state here as interrelated testable hypotheses: (1) larvae drift slowly and passively from the spawning area to the northwest and form a persistent accumulation northeast of the Bahamas, and (2) larvae are introduced over a period of several months into the Gulf Stream system largely north of the Bahamas.

If these hypotheses are correct, they go far in explaining how larvae can be distributed the length of the North American east coast at the same time and in the same stage of development, ready for metamorphosis and migration into freshwater. This question had puzzled us for some time prior to development of the model and to

publication of some recent physical-oceanographic studies.

A strong Antilles Current, if it exists as the classical picture suggested, would seem to sweep larvae quickly into the Gulf Stream and hence beyond the waters of North America. However, recent work by Ingham (1975), Gunn and Ingham (1977) and Gunn and Watts (1982) has called into question the existence of an Antilles Current. Rather, the area is apparently one of eddy variability with only slow overall net flow to the northwestward, at least during summer.

In the most recent paper on the subject Olson, Schott, Zantopp and Leaman (1984) show an anticyclonic circulation cell in the upper 1000 m northeast of the Bahamas. This circulation cell bears a striking resemblance to our modeled patch of larvae. Most of the water from the presumed spawning area (and hence most the larvae) would enter the Gulf Stream north of the Bahamas via this circulation cell.

The second approach to the question of larval drift was through the historical data which allowed us to plot bimonthly distribution of leptocephalus captures (Kleckner and McCleave, in press). Although these plots are strongly influenced by fishing effort, the gradual movement of 0-group larvae into the Gulf Stream which was suggested by the model is generally reflected in these data. The predicted concentration of larvae northeast of the Bahamas does not show in these bimonthly plots, but the area has been singularly avoided by those seeking eel larvae or anything else biological.

The historical data have, however, provided good evidence in support of the idea that most larvae enter the Gulf Stream north of the Bahamas rather than through the Bahamas and Straits of Florida. In the samples examined were a fortuitous set of four transects across the Stream made by R.H. Backus and J.E. Craddock in late July and early August 1978. They fished a multiple opening/closing net system with appropriate mesh size for leptocephali of that age.

We found in those collections that leptocephali of the American eel increased in abundance from < 2 per 10^4 m^3 of water strained at the southernmost transect to usually $2-18$ leptocephali per 10^4 m^3 at the two northernmost transects (off Cape Romain and Cape Hatteras) (Fig 11) (Kleckner and McCleave 1982). Furthermore, at Cape Romain and Cape Hatteras the abundance of leptocephali in tows characterized by Sargasso Sea mesopelagic fish fauna was roughly threefold greater than in those tows characterized by Gulf Stream fauna. These findings are in agreement with increased volume transport of the Gulf Stream north of the Bahamas due to Gulf Stream recirculation predicted by Stommel, Niiler and Anati (1978), Fiadeiro and Veronis (1983) and others.

Our first approach, modeling, yielded testable hypotheses, with which information from our second approach, examination of historical data, is consistent. The third approach to this problem was a direct test of the hypotheses on cruises in July and September 1984, when we made transects across the Gulf Stream and through the area of concentration predicted by Power and McCleave (1983). The relative abundance and size distribution of leptocephali when analyzed in conjunction with water-mass identification and associated fauna should provide a conclusive test of the predictions.

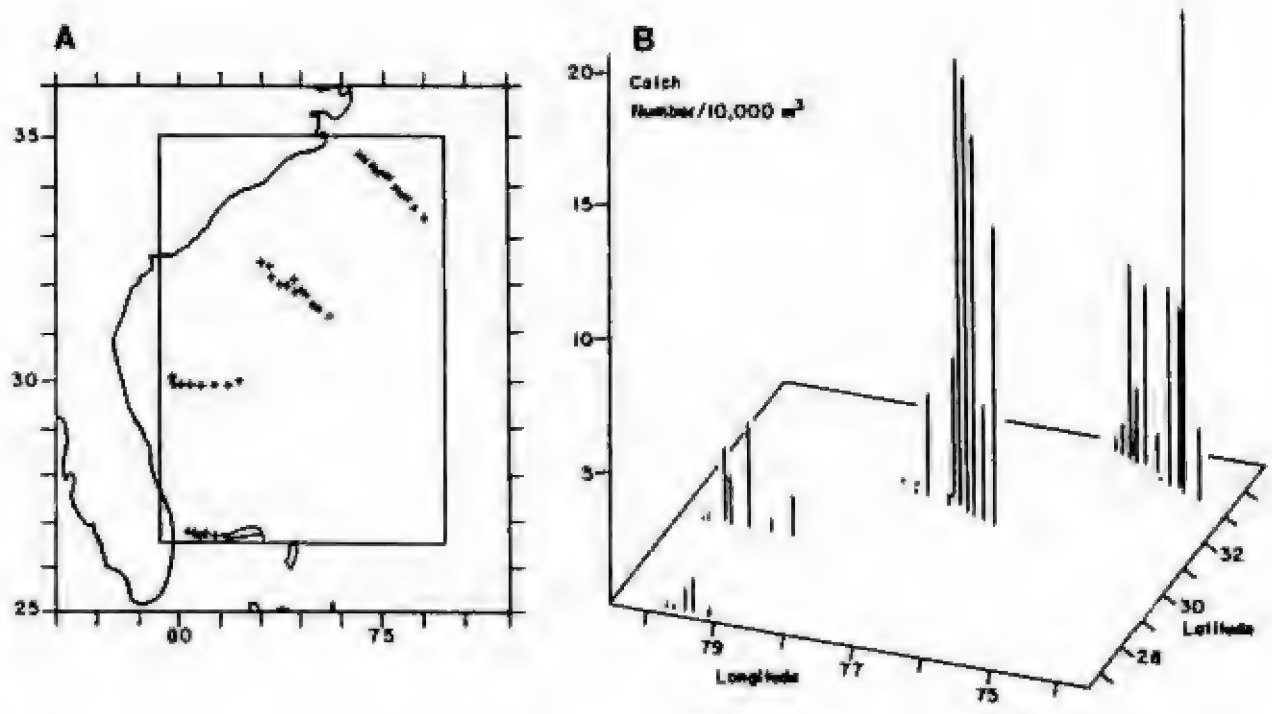

Figure 11

A. Station locations on four transects of the Florida Current (Gulf Stream system). B. Numbers of American eel leptocephali caught per 10^4 m^3 of water strained at the transect stations. (From Power and McCleave 1983; data from Kleckner and McCleave 1982.)

EPILOGUE

This paper, though speculative, points to several advances in our understanding of the oceanic migration of Atlantic ***Anguilla***. However, it in no way alters the conclusion reached by Schmidt (1912, p. 636) when he first suggested in *Nature* the heresy that spawning of the European eel might occur in the Sargasso Sea: "Altogether, the whole story of the eel and its spawning has come to read almost like a romance, wherein reality has far exceeded the dreams of phantasy."

ACKNOWLEDGMENTS

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MIGRATION AND UTILIZATION OF ESTUARINE NURSERIES BY JUVENILE FISHES: AN EVOLUTIONARY PERSPECTIVE

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ABSTRACT

The most successful fishes of the southeast Atlantic U.S.A. migrate to use estuaries as juvenile fish nursery areas. These and other migrations serve to maximize surplus power, which in turn is related to fitness (= lifetime reproductive output). Analysis of the costs and benefits of estuarine nursery areas suggest that surplus power is gained by juvenile fish that tolerate variable estuarine abiotic conditions rather than avoid extreme conditions as adults may do. The principle advantages of estuaries to juvenile fish may be more favorable temperatures, lower risk of predation and, probably, a competitive advantage for food. Migrations by larvae are expensive because power reserves and vagility are low; larvae may not be able to make certain migrations without assistance from currents. Survival in early stages is a major determinant of fitness, but predation pressure is not readily assessed in terms of surplus power. Until quantitative links between surplus power acquisition at different life history stages are established, the fitness of the predator avoidance component of this life history strategy will be difficult to determine.

INTRODUCTION

Migration in fishes should be considered from the perspective of costs and benefits. Feeding migrations determine the net gain of foraging activity, but spawning migrations constitute the consummation of fish life histories and may thus be more closely related to fitness. Costs of migration are difficult to assess. Because fishes may employ a variety of tactics for migration, costs probably will have to be determined for each particular type of migratory behavior.

Bioenergetic Costs and Benefits

Cost-benefit analyses have been applied to a variety of fish behaviors. Feeding behaviors have been quantitatively evaluated using optimal foraging theory (Pyke, Pulliam and Charnov 1977). An important assumption of this theory is that overall fitness of an animal increases as a function of net rate of energy intake. Numerous tests of hypotheses of optimal foraging in fishes have generally supported this idea (e.g., Werner and Hall 1974, Kislalioglu and Gibson 1976). Recent work (Ware 1975, 1978; Mittelbach 1981) has included better estimates of the actual costs of foraging than were available in earlier tests.

Behavioral thermoregulation in ectotherms has also been subjected to cost-benefit analyses (Huey and Slatkin 1976; Magnuson, Crowder and Medvick 1979). In this case, the "currency" to be maximized was the net rate of energy gain, which would presumably maximize fitness. The range of final preferred temperatures in a fish correlates well with the optimal temperatures for many physiological processes in that species (Brett 1971) as well as for growth (Magnuson et al. 1979, McCauley and Casselman 1980). Most studies of behavioral thermoregulation in fishes, however, have not treated the behavior in terms of cost-benefit analysis, they have not included all the appropriate costs and benefits. For example, few field studies of thermal habitats of fishes relative to their preferred temperature in laboratory studies have included availability of food or the presence of competitors or predators (Crowder and Magnuson 1983). Failure to include appropriate energetic costs, competitors and predators has also constrained foraging theory (Dill 1983).

The Concept of Surplus Power

Ware (1982) has sought to unify such approaches to fish behavioral strategies and to respond to critics of the optimization approach. His intent was, "To consider some of the evidence we have for believing that natural selection increases the frequency of certain phenotypic traits determining foraging success and fitness, in the direction implied by optimization arguments." Ware's approach is based directly on fish bioenergetics—using an energy balance equation, he elaborates the concept of "surplus power" which has dimensions of energy per unit time. He argues that natural selection "operates to increase surplus power" and thus will favor behaviors that improve power acquisition (e.g., optimal foraging), that conserve power (e.g., optimal swimming behaviors), and that allocate surplus power to growth and reproduction (e.g., optimal life history strategies) such that fitness is actually maximized. Ware's conception succeeds where previous attempts have failed not just because he has identified a reasonable currency (energy·time^{-1}), but also because he proceeds to map surplus power into growth and reproduction such that fitness is maximized. While other approaches have assumed a correlation between growth and fitness, Ware (1982) employs the theory of life histories to allocate power in ways that actually maximize fitness.

Migration has measurable (in theory at least) costs and benefits. In this paper we consider the adaptive significance of migrations of immature fishes that utilize estuaries as nursery areas. We also consider whether or not larval or juvenile fish could accomplish these (or other) migrations without assistance from favorable currents. The tactics of such current-assisted migrations have been aptly reviewed by Arnold (1981). We, however, consider these questions from a fitness (strategic) perspective.

COSTS AND BENEFITS OF ESTUARINE NURSERY UTILIZATION

Estuaries and Their Fishes

Estuaries, in the broadest sense, include habitats ranging from inshore shelf waters (McHugh 1966) to the heads of drowned river valleys, fjords, and hypersaline lagoons. Because such a variety of hydrographies are included between rivers and the ocean, and because hydrographic conditions drive many of the important abiotic variables, little insight into "estuarine systems" is likely without explicit recognition of the physics of water movements. Compared to stenohaline marine or freshwater systems, estuaries are abiotically variable (Stickney 1959) and therefore may be rigorous environments. Species that inhabit estuaries must be able to tolerate or avoid wide ranges of salinity, temperature, dissolved oxygen and high levels of turbidity. Where estuaries are separated from the ocean by shallow bars or barrier islands, currents are generally unpredictable, being driven mainly by wind, not lunar tides.

Most of the data we present in this paper were collected from the Pamlico River and Sound estuary, North Carolina (Fig 1). This is a shallow lagoon system separated from the nearshore shelf waters by barrier islands. Exchange with the ocean is through narrow inlets, so the lunar tidal influence is minor. The Pamlico system is shallow, usually well-mixed vertically, and currents are dominated by winds which rotate 360 degrees annually (Miller, Reed and Pietrafesa 1984).

The juvenile fish in estuaries are derived from three sources. One group is comprised of marine anadromous fish which make spawning migrations into freshwater; the eggs hatch and the developing larvae drift downriver and arrive in estuaries as juveniles, (e.g., striped bass (***Morone saxatilis***), alosines and salmonids). The second pattern involves an offshore spawning migration by adults which is followed by an inshore migration by larvae or juveniles to the estuaries. On the Atlantic and Gulf coasts of the USA, nearly 80% of the commercial fisheries catch (by weight) consists of species which spawn in the ocean and have a juvenile estuarine phase (Fig 1). Spot (***Leiostomus xanthurus***), croaker (***Micropogonias undulatus***), menhaden (***Brevoortia tyrannus***) and flounders (***Paralichthys*** sp.) are included in this group, as well as penaeid shrimp and blue crabs. Third, a number of species reside yearlong in the estuaries, so utilization of estuaries does not involve an extensive migration from either fresh or offshore marine waters (e.g., anchovies, ***Anchoa*** sp., hogchokers, ***Trinectes maculatus***, and killifish, ***Fundulus*** sp.). With few exceptions the dominant and commercially important species in estuaries undergo spawning

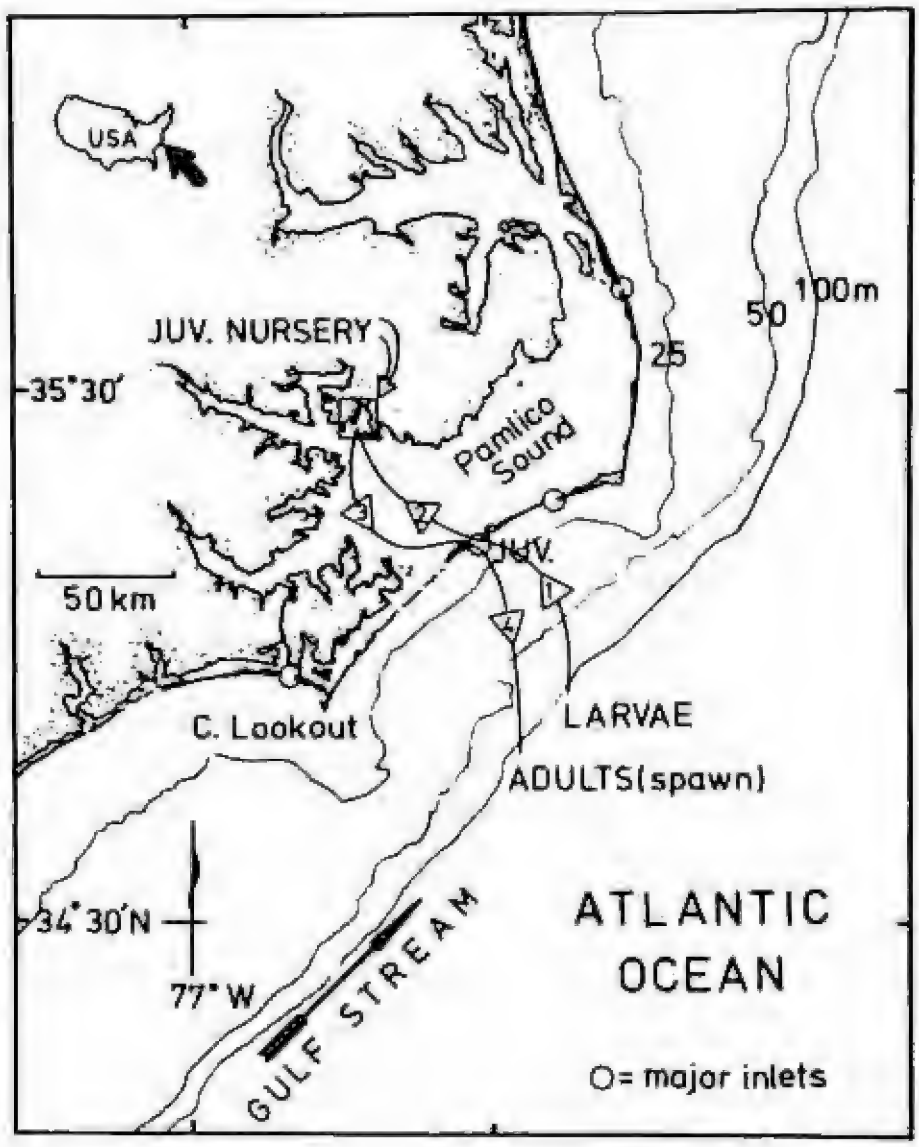

Figure 1

Migration route of dominant commercial species utilizing estuarine nursery area (Rose Bay, Pamlico Estuary, NC). Larvae (1) and juveniles (2) migrate in winter and early spring. Sub-adults (3) and adults (4) migrate in fall and winter.

migrations.

Migration and Surplus Power in Juvenile Estuarine Fishes

Many migratory fishes in North Carolina estuaries migrate upriver to spawn. Juveniles of these species are found in the estuary mainly in late spring and summer and move offshore as temperature declines in fall. Juveniles of a smaller group of species originate from eggs spawned offshore in fall or winter (Miller et al. 1984) and enter the estuary in late winter or early spring. Thus, two different migratory patterns of adults are involved: upriver and offshore. The larvae or juveniles of anadromous species can "drift" downstream into the estuary. Larvae and juveniles which originate offshore may "drift" inshore. Recent hydrographic data suggest that the most favorable shelf current regime for shoreward transport is during the winter (Miller et al. 1984). Larvae could remain in the appropriate current layer by simply selecting the warmest temperature available in the vertical dimension. Other advantages of winter spawning offshore might include lower risk of predation and longer survival time if food were limiting. Can bioenergetic arguments help explain

the "migration" of these juveniles that were spawned offshore?

Energetic Costs of Migration

Although estimates of the direct costs have been made for some migrations, they generally have not been made in the context of overall fitness assessments. In the case of larval and juvenile fish, the possibility of their incurring significant costs is implicitly recognized when considering tidal stream transport as a potential energy-saving mechanism (Weihs 1978, Arnold 1981). However, it has not been considered whether or not larval or juvenile fish could make unassisted migrations over substantial distances and times. Certainly no one has investigated this question in the context of overall fitness or surplus power (Ware 1982). Considering that small fishes are unable to store significant quantities of energy for such migrations and that they are apparently more vulnerable to predation if they do not allocate most of their surplus power to growth (Werner and Gilliam 1984), establishing the limits of their migratory capacities seems to be a worthwhile exercise.

As an example of power allocation during a larval fish migration, consider the approximately 100 km migration made by immature spot and croaker. These fish move from their winter spawning areas near the Gulf Stream off North Carolina to the inlets of Pamlico Estuary (Fig 1). This migration takes about 50 days, during which they grow from about 2 mm (SL) at hatching to about 15 mm (Miller et al. 1984). Using 0.25 cal $\cdot g^{-1} \cdot h^{-1}$ (Beamish 1978) as an estimate of the cost of swimming for small fish and integrating over their growth from about 10^{-5} to about 0.016 g (dry weight), we estimate the total cost of the migration is about 4 cal. In another analysis based on Schmidt-Nielsen (1972), Beamish also calculated swimming cost in terms of cal $\cdot g^{-1} \cdot km^{-1}$. Extrapolating his curve to small fish, we arrive at an estimate of about 10 cal $\cdot g^{-1} \cdot km^{-1}$. These calculations yield an integrated total cost for the same migration of about 6 cal when the daily movement rates of growing larvae are summed over different size fish that are swimming at 1 BL$\cdot sec^{-1}$. Using Beamish's curve for total energy expenditure and summing daily rates during the 50 day migration results in an estimate of about 12 cal (= 4 for swimming + 8 for other metabolic costs). A 15 mm fish has a body caloric content of about 80 cal (Thayer, Shaaf, Angelovic and LaCroix 1973), so the apparent allocation of power was 80 cal for growth, 5 (4−6) cal for swimming and 8 cal for other metabolic costs: total = 93 cal. All of these are approximations since it was necessary to extrapolate well outside the published curves to make estimates for very small fish. The growth of fish from 2 mm to 15 mm in 50 days is an instantaneous daily ponderal growth rate of about 0.12 according to the formula:

$$G_d = \frac{(\ln wt_{d=50} - \ln wt_{d=1})}{50} \qquad (1)$$

So, the above apportionment of surplus power into metabolism and growth would not seem unreasonable. However, at a swimming speed of 1 BL$\cdot sec^{-1}$, the assumed rate in the above calculations, the fish could only swim about 28 km in 50 days.

If the fish swam at about 4 BL·sec^{-1}, they could swim the 100 km in 50 days. Using Beamish's curve, this would raise the cost of swimming approximately 10-fold (to about 40 cal). In fact, if these calories were diverted from growth, then the fish, having grown less, would need to swim faster than 4 BL·sec^{-1} to cover the distance in 50 days. To add, through ingestion, the necessary additional 35 calories for swimming at 4 BL·sec^{-1} without sacrificing growth would require an average increase of about 40% in surplus power. The question then might be one of whether or not they could ingest the necessary food during the migration, particularly while swimming at a mean rate of 4 BL·sec^{-1}. Since allocation of power to growth results in increased swimming speed, there may be for any migration an optimal pattern of growth and swimming such that the larvae grow as long as possible (to a critical size?) without actively migrating, thereby minimizing the time required for the migration. In addition to power savings and (presumably) more time for feeding, minimization of migration time could also result in reduced exposure to predation during the migration.

We conclude, both from the point of the required swimming capacity and the necessary magnitude of increase in surplus power to support it, that it is unlikely that these larvae could make the 100 km, 50-day migration unassisted by currents. Thus, while increases in swimming efficiency, e.g., by streamlining, or in feeding efficiency would help, the limited storage capacity and vagility of the larvae and the apparent high larval growth requirement suggest that there is an upper limit to the migrations they can possibly make without assistance from currents. In particular it seems unlikely that any larvae of fishes spawned near the Gulf Stream off North Carolina *could* migrate to inlets in any season other than winter, when the current regime appears to favor onshore larval transport (Miller et al. 1984).

Therefore, before we ask why larval fish do not make certain migrations, we should ask whether or not it is possible for them to do so. In most cases this would seem to require additional resolution of the hydrography, since opposing currents, for example, would greatly increase the costs of any migration. As fish grow, their swimming capacity increases rapidly. In the above example the fish swam only 8 of the 28 km travelled during the first 25 days. While swimming speed increases linearly with length, potential surplus power increases as a cubic function of length, and specific growth and metabolic rates decline. These high metabolic demands and lack of reserve power in early larval fish may preclude even tidal stream transport (Weihs 1978) if the fish must "sit and wait" for tidal currents to reverse direction.

During the second leg of their migration, from the inlets to the nursery areas (Fig 1), juveniles grow from about 15 to 20 mm (0.016 to 0.038 g dry weight)—a net caloric gain of about 100 cal. Even though they are capable of making this migration unassisted in 30 days swimming at 1 BL·sec^{-1}, they may not. Winter, wind-driven, bottom currents in Pamlico Sound (see Miller et al. 1984) could transport them in 5−7 days—a substantial energy savings which could be allocated to growth. Riding currents vs. swimming unassisted translates into a potential increase in instantaneous total growth rate of about 0.09. Riding currents may be a considerably better strategy both in terms of increasing surplus power and in minimizing risk of predation. However, it should be remembered that the above calculations were necessarily based on extrapolation from data for larger fish, so it is important to re-emphasize that these are ***possibilities*** only.

Advantages of Early Arrival in Estuarine Nursery Areas

Thermal—Shallow temperate estuaries like the Pamlico warm more quickly in spring than do offshore waters, reach higher summer maximum temperatures, and cool more rapidly in the fall (Fig 2). The maximum differences occur in March and June (about 4°C) when the estuary is warmer than the nearshore shelf waters and in winter when the shelf waters may be as much as 7°C warmer than the estuary. Assuming warmer temperatures are energetically advantageous, juvenile fish should be offshore until about February or March when the spring "crossover" occurs and in the estuaries until about August or September when the fall "crossover" occurs. For most of the spring and summer, the thermal "advantage" of estuaries is about 2°C. Late summer temperatures in temperate estuaries may occasionally exceed the optimum temperature for some species but are usually not in excess of 30°C. Juvenile fishes which migrate from the ocean in winter and early spring arrive in the estuary and start growing before many of the estuarine species which spawn in spring and summer even hatch. This may allow some advantage in early access to food and may also allow these migratory species to grow larger before predation by fishes becomes a more important factor due to seasonal warming. In addition to the presence of greater numbers of adult fish predators in the estuaries in summer, the metabolic costs and (presumably) feeding rates of these predators also increase with the increase in water temperatures.

Food—Estuaries are widely regarded as among the most productive of aquatic systems in the world (Whittaker 1975, Mann 1982), and it is reasonable to suppose that they could provide more food for juvenile fish than either freshwater or offshore marine systems. However, it is also likely that production, per se, is not always available as appropriate food. As numerous recent studies have shown, the ***availability*** of food (appropriate particle size, etc.) is an important determinant of fish production (cf. Nilsson 1978, Lasker 1975). We also know little about the foraging behaviors of juvenile estuarine fishes or specifically what their requirements are relative to food size or taxa. Unfortunately, neither the basic productivities nor the particle size distributions have been determined in a manner which would permit comparison of estuaries with their adjacent freshwater or marine systems in terms of fish food availability. We could suppose that secondary production in estuaries may be more benthic and offshore systems more planktonic. Also, we might guess that an additional source of food in estuaries is supplied from upstream or the surrounding wetlands, but again, the relevance of these possibilities to juvenile fishes is mostly speculative. Odum and Heald (1975) present convincing evidence that mangrove-derived detritus may be important to some fishes. Salt marshes have been reputed to export detritus to estuaries, but the significance of this to secondary consumers has been questioned by Haines (1979). Before we can make significant progress on assessing the costs and benefits of estuarine nursery utilization relative to food, a substantial amount of research will be necessary on both the foraging requirements of the fish and characteristics of the availiable food.

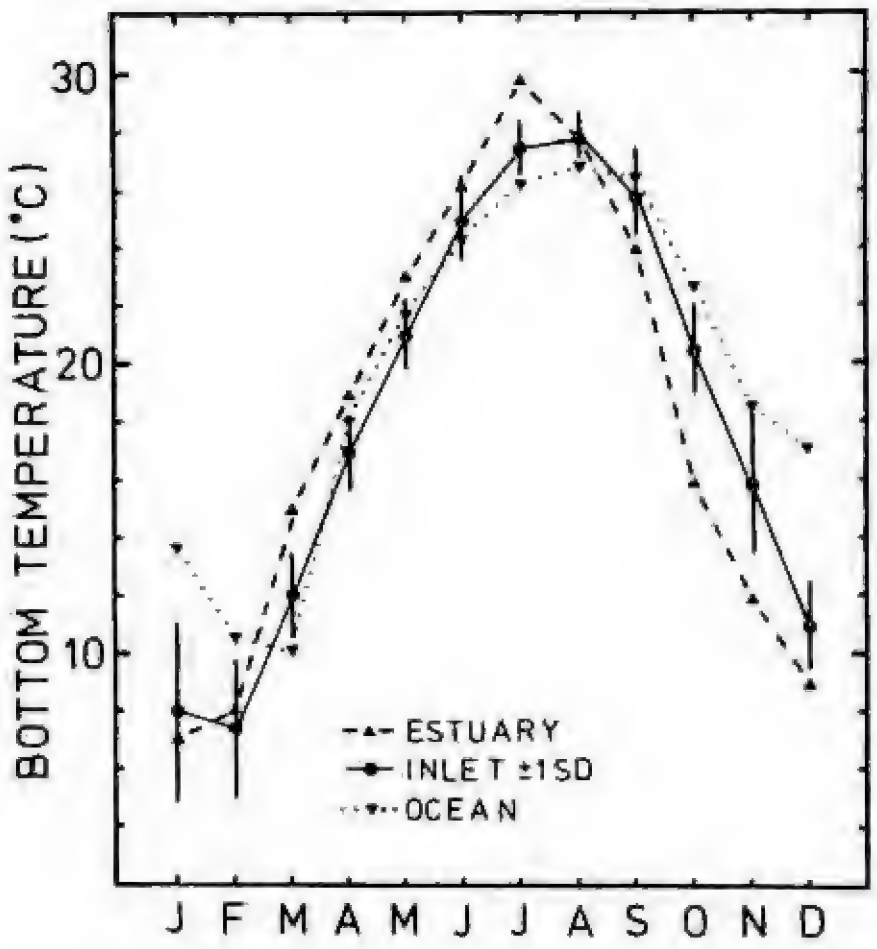

Figure 2

Mean monthly bottom temperature. Ocean = 0–20 m isobath, 33–34°N off North Carolina (1945–1982). Inlet = Beaufort, NC (1974–1982). Estuary = Rose Bay, Pamlico Estuary, NC (1982).

Energetic Costs of Tolerance vs. Avoidance

Fish which inhabit estuaries are exposed to extremes of temperature and salinity as well as to rapid fluctuations in these parameters. Estuaries are therefore generally considered to be abiotically stressful habitats (Miller and Dunn 1980). However, large numbers of young fish use estuarine nursery grounds, suggesting that the advantages of migrating there outweigh the costs of living in suboptimal abiotic conditions. The costs of tolerance have not yet been determined relative to the costs of swimming to avoid stressful conditions. If these fish are able to tolerate estuarine conditions for relatively low costs, they could increase surplus power and grow faster than less plastic fish which must invest power in avoidance behavior.

Unfortunately there is little bioenergetic information on estuarine fishes and virtually no data on small (< 10 g) individuals. Oxygen uptake measurements on larger ***Tilapia nilotica*** (Farmer and Beamish 1969) and ***Oncorhynchus nerka*** (Brett 1964) were used here to determine costs relative to standard metabolism (STM) at 11.6 ppt salinity and 25°C (Fig 3). Costs of swimming at 3 $BL \cdot sec^{-1}$ were over 4 times those of STM at this salinity and temperature. Salinity tolerance, defined here by acclimation to 30 ppt at 25°C, required roughly 1.5 times STM costs, and acclimation to a 5°C elevation in temperature was about 0.8 the STM costs. These conditions (30 ppt and 30°C) were chosen as examples of temperate estuarine extremes and 3 $BL \cdot sec^{-1}$ as the maximum sustained swimming speed (Beamish 1978). Clearly, large differences in these relative costs can be expected for different swimming

speeds, species and sizes (Nordlie and Leffler 1975, Rao 1968, Wohlschlag and Wakeman 1978). Younger fish probably incur even higher swimming costs and lower tolerance costs than adults (Beamish 1978, Holliday 1965). Preliminary oxygen consumption studies on the response of juvenile spot to salinity changes of over 20 $ppt \cdot h^{-1}$ indicate that tolerance costs are relatively low (Moser, unpublished data).

Estuaries are often horizontally, rather than vertically, stratified with respect to temperature and salinity. Thus, fish must move farther in estuaries to behaviorally adjust than they would, for example, in lakes. This too would make escape in the face of suboptimal abiotic conditions less favorable for estuarine fish. Because swimming costs may exceed tolerance costs by a factor of > 3 (Farmer and Beamish 1969), juvenile estuarine fish may be adapted to tolerate stressful environmental conditions rather than fleeing them. If this strategy is indeed followed, estuaries are not as costly for catadromous postlarvae to inhabit as has generally been supposed.

Refuge from Predation

Adult fishes are, in general, less able to tolerate certain environmental extremes than their respective younger stages (Holliday 1965, Magnuson et al. 1979). Certainly many stenohaline marine and freshwater adult fishes do not inhabit estuaries. It follows from these generalizations that fish predation pressure on juveniles in estuaries may be lower than that in marine systems. Again, however, this has not been quantified adequately. Vast numbers of ctenophores and jellyfish are often found in estuaries, while other potentially important predators such as chaetognaths and predatory amphipods seem to be more abundant in marine waters.

Three characteristics of estuaries may make them refugia for juvenile fish. Turbidity reduces encounter rates with prey in visually feeding fishes (Vinyard and O'Brien 1976) and may thus reduce overall predation risk to juvenile fishes in turbid habitats. Secondly, habitat structural complexity (e.g., in estuarine grass beds) also reduces predator efficiency (Glass 1971; Ware 1972; Vince, Valiela, Backus and Teal 1976; Van Dolah 1978) and thus may provide a refuge from predation for juvenile fishes. Finally, shallow water may also provide protection as relatively large predators are less common in shallow water. By contrast, the open ocean or continental shelf is a relatively deep, clear, structurally simple habitat where the efficiency of visual predators would potentially be much higher. Both spot and croaker juveniles in the Pamlico Estuary tend to occupy the shallow, low salinity habitat in the upper ends of the bays, but spot are more common in deeper, higher salinity areas. We obtained data from the North Carolina Division of Marine Fisheries (Steve Ross, personal communication) from their 1981–1983 surveys of juvenile fish abundance in the Pamlico Estuary. Comparison of the apparent May–July instantaneous daily growth and mortality rates of spot and croaker in 7 high (mean = 26.7 ppt) and 8 low (mean = 13.3 ppt) salinity nursery areas in the Estuary showed the following relationships. Croakers experience lower mortality rates than spot throughout the Estuary ($Z = -0.0163$ vs. $Z = -0.0271$). Both experience lower mortality rates at low salinity ($Z = -0.0206$ vs. $Z = -0.0227$ in high

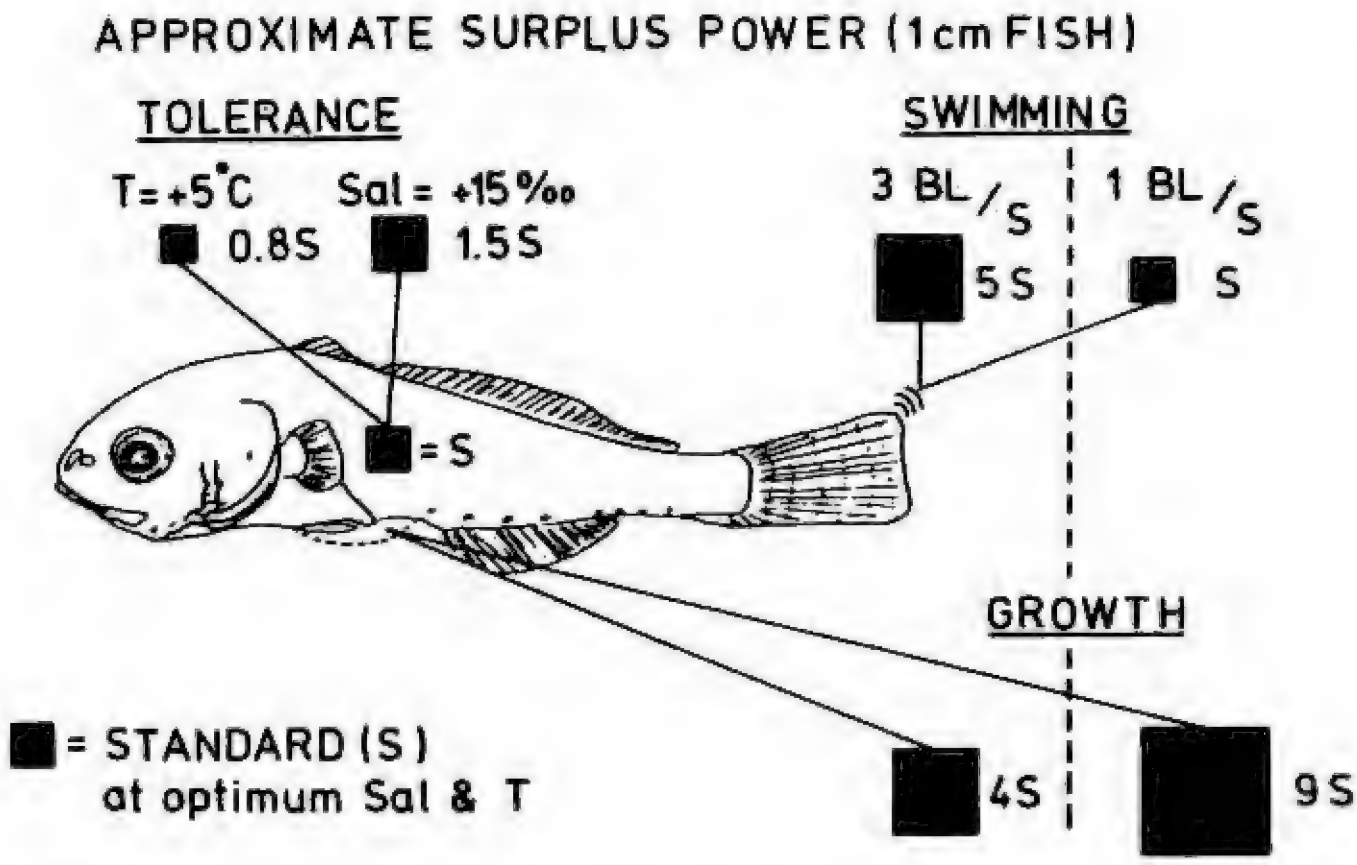

Figure 3

Distribution of potential surplus power for a small fish showing approximate relative costs of tolerance, swimming and growth in multiples of standard metabolism. Also shown is the approximate amount of surplus power available for growth at two swimming speeds.

salinity). This may be linked to lower predation pressure in the shallow, low salinity habitats. Croaker grew slightly faster than spot at low salinity ($G = 0.0295$ vs. $G = 0.0229$). However, overall differences in growth rates of these two species in the two habitats were probably negligible.

A basic problem when considering risk of predation along with behavioral and life history adaptations of fishes is that the latter can be readily measured in terms of surplus power, but risk of predation is not easily expressed in energetic terms. How does one equate predation risk with foraging opportunity in a particular habitat? Because fishes which forage at one trophic level are also the prey of the foragers a level above, they must balance risk of predation with energetic return via foraging. Increasing evidence suggests that prey accept reduced foraging opportunity to avoid predators (Sih 1980; Mittelbach 1981; Dunbrack and Dill, in press; Werner and Gilliam 1984). But arriving at a "currency" to express risk of predation in energetic terms is difficult. Dill (in press) has outlined two approaches: in the first, the animal could be presented with various combinations of risk and energetic reward—the amount of risk the animal is willing to tolerate for a given energetic reward, or the amount of energy gain the fish is willing to forego, would provide an energetic "index" of how the fish ranks risk in energetic terms. Second, the effects of both risk and energy intake on some direct measure of fitness could be estimated. An appropriate measure would be that suggested by Ware (1982)—lifetime reproductive output, which integrates age-specific fecundity and age-specific mortality. Because both fecundity and mortality due to predators are size dependent, the pattern of surplus

and reproduction is critical.

Predators can of course alter prey behaviors other than foraging behaviors (which affect the ingestion term in the energy balance equation). Predators could affect both standard and activity metabolism if they force the prey to occupy a physiologically sub-optimal habitat or if the prey are frequently avoiding predation and thus expending a substantial amount of energy on burst swimming to escape predators. These effects, in addition to the above-mentioned effects on foraging, would act to reduce surplus power. Power allocation would, of course, also depend on predation as it influences age-specific fecundity and mortality schedules (Ware 1982).

DISCUSSION

In this paper we have discussed the behaviors of individual fishes from the perspective of surplus power. But surplus power is just an "interim measure of fitness" (Ware 1982) and does not necessarily relate directly to reproductive value.

The exact relation between contemporary behaviors of individuals and the ultimate reproductive value associated with those behaviors is difficult to establish except in the most general form. For example an apparently "costly" behavior in the short term may have substantial "payoffs" in the long term. Another constraint on the application of these ideas is that some processes such as predation risk are not easily expressed in terms of power. Further, at this point our understanding of power allocation to growth and reproduction is sketchy; the theory of optimal life history strategies is a start.

Trade-offs occur in allocating surplus power to growth and reproduction. Early in the life of fishes, most surplus power is allocated to growth; later, as a function of age-specific mortality schedules, increasing amounts of power are allocated to reproduction. In our analysis of migrations of juvenile fishes an interesting question arose. Should larval fishes start migrating at a small body size and grow slowly along the way, or should they allocate all their surplus power to growth, attain a larger body size and then begin migrating? Because swimming speed and costs of transport are body size-dependent, this becomes an important question.

Adult fishes that allocate substantial power to migration have less surplus power to allocate to eggs and sperm. Unfortunately, we do not understand well either the costs (direct and indirect) of spawning migrations or the benefits to the offspring of being placed in a particular habitat (relative to some alternative, at least on an evolutionary time scale). The direct costs of migration in juvenile fishes may be assessed by knowing the standard metabolic costs of occupying the various habitats along the migration route and by assessing the costs of transport. We know much more about the standard costs and suspect that at least for larvae the activity costs are minimized by larval transport. Indirect costs of larval migrations may include increased risk of predation while moving. Energetic costs may be similar in adults, and it is possible that migrating adults use similar cost reducing strategies (e.g., riding currents). One indirect cost of migration in adults is, perhaps, increased mortality due to fishing.

The benefits of migration are based on relatively poorly known favorable "opportunities" in the new habitat. We thought that the migrations of juvenile fishes into North Carolina estuaries would have more readily identifiable benefits. Though we have reason to believe that the benefits may be high, the data to support this hypothesis are limited. The spawning migrations of the adults may have more obvious benefits for the offspring in terms of placing them in a "better" larval habitat, placing them in a position for larval transport, and early arrival in the estuary.

Our preliminary data suggest that juveniles of dominant species may not, in fact, be stressed as much as we expected. The prevailing concept of estuaries as stressful environments needs reexamination. Similarly, the concept of "estuarine-dependence" in these fishes requires clarification. Clearly, many species have adapted to the variable environment of estuaries. Indeed, many species seem to be most abundant in estuaries, but dependence, in the sense that estuaries are an essential habitat, is more difficult to test since most of the species that inhabit estuaries are also found in marine waters. It may be that these species are dependent on estuaries in the same way that certain species of birds (supertramps) are dependent on early successional stages of islands (Diamond 1975). Whether these fishes would be competitively inferior to the inhabitants of, for example, the more stable marine environments, is debatable. Concepts such as surplus power allocation lead to testable hypotheses which can direct data collection on juvenile fish distributions in estuaries. There seems to be adequate reason to suspect that immature and adult fish may respond differently, both physiologically and behaviorally, to their respective biotic and abiotic environments. But our understanding of the responses of juvenile fishes, in particular, is poor.

Fishes employ a wide variety of life history strategies. In summary, we suggest that: 1) migrations serve to maximize surplus power; 2) larvae need currents to migrate—juveniles do not, but may use them to increase surplus power; 3) juveniles in estuarine nursery areas add surplus power through tolerance of environmental variation, not avoidance; and 4) estuaries also increase surplus power in juvenile fishes by providing refuge from adult predators that are less able to tolerate environmental variation. A greater understanding of these patterns would help us separate those strategies or behaviors we may expect to see, based on their consistency with natural selection, and those which may perforce be less likely.

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HOMING AND THE EVOLUTION OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*)

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ABSTRACT

The great majority of adult Pacific salmon (*Oncorhynchus* spp.) that survive to maturity spawn in the stream where they were incubated as eggs and reared years earlier. While the mechanisms underlying this homing migration have been intensively studied, the evolutionary benefits and costs of homing have received relatively little attention. In considering homing from an evolutionary perspective, this paper (1) reviews evidence for homing in sockeye salmon, (2) examines the extent to which populations of this species are specialized for their river-lake systems, (3) proposes three factors that may influence the occurrence of straying in salmon populations and species and (4) discusses the importance of straying in establishing the current distribution of salmon following the Wisconsin glacial period, roughly 10,000 years ago.

INTRODUCTION

It is now well known that most Pacific salmon (genus *Oncorhynchus*) that survive to maturity return to spawn in the stream from which they departed years earlier as juveniles. This phenomenon is referred to as homing. Many studies have examined the sensory mechanisms underlying the homing of salmon, but the evolution of homing has seldom been considered. Recently, Quinn (1984) proposed that homing and straying may be in dynamic balance in salmon populations. According to this hypothesis, the rates of straying (spawning in non-natal rivers) should vary according to the characteristics of the rivers and species involved. Thus straying is not viewed as chance dispersal but rather as part of a genetically coded reproductive strategy.

The relative homing tendencies of salmon species have been discussed in the literature (for example Hanamura's (1966) comparison between Asian sockeye *Oncorhynchus nerka* and pink salmon *O. gorbuscha)*. Unfortunately, reliable estimates of homing and straying in salmon populations are almost nonexistent. Wild populations are difficult and costly to study, and data from hatcheries are not always applicable to natural systems. Moreover, straying estimates have usually been based

on recoveries of salmon at one-way traps. Since it is known that some salmon will ascend non-natal streams but eventually spawn in their home river (Ricker and Robertson 1935, Ricker 1972), many estimates of straying may not be accurate. This absence of high quality data has rendered all discussions highly speculative. The purposes of this paper are to (1) review past work and present new data on homing in sockeye salmon, (2) summarize evidence that sockeye populations have become specialized for the river-lake systems where adults spawn and juveniles rear, and (3) discuss the evolutionary benefits and costs of homing in Pacific salmon.

EVIDENCE FOR HOMING IN SOCKEYE SALMON

A number of marking studies were conducted at the beginning of the 20th century to test the hypothesis that sockeye salmon return as adults to the stream they left as juveniles (reviewed by Foerster 1968). By far the most conclusive experiments were conducted at Cultus Lake, British Columbia (Foerster 1936, 1968). In the spring of 1931 the lake's entire population of 365,265 smolts (seaward migrating yearlings) was marked by removal of both ventral fins. In the fall of 1933, when these fish were expected to return as adults, 2856 marked large fish were recovered along with 409 small unmarked fish and 17 large unmarked ones. The 409 small sockeye were almost certainly fish that went to sea in 1932 and so were not marked. Some of the 17 large unmarked fish could have escaped marking in 1931 or their fins could have regenerated. At most the rate of straying into Cultus Lake was 0.6% (17/2873), in spite of the fact that most of the sockeye salmon returning to tributaries of the Fraser River must bypass Cultus Lake to reach their natal streams. This marking experiment was repeated with smolts leaving Cultus Lake in 1936 with the following results: of 497,598 marked smolts, 8980 large marked sockeye returned in 1938 along with 4226 small unmarked fish and 136 large unmarked salmon for a maximum straying rate of 1.5% (136/9116).

Since Foerster's studies, no other large-scale marking experiments have been conducted with natural sockeye salmon populations. Capturing and marking large numbers of smolts is very expensive and time-consuming, as is the job of inspecting adult fish for marks. However, a recent discovery by Dr. Leo Margolis (Dept. of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C.) permits examination of homing in certain sockeye populations without having to mark the smolts. During the one or more years that juvenile sockeye salmon spend in a lake prior to seaward migration, they may become infected with a variety of internal parasites. When these parasites are found in one sockeye nursery lake but not another, they constitute a potential biological tag.

The use of parasites for stock identification is not a new concept (Margolis 1963, Sindermann 1983), but recently a parasite particularly useful for stock identification has been found in sockeye salmon. A myxosporean protozoan *Myxobolus neurobius* infects the brains of almost all smolts leaving Sproat Lake but virtually none of those leaving nearby Great Central Lake, both tributaries to the Somass River on the west coast of Vancouver Island, British Columbia (Fig 1). Since

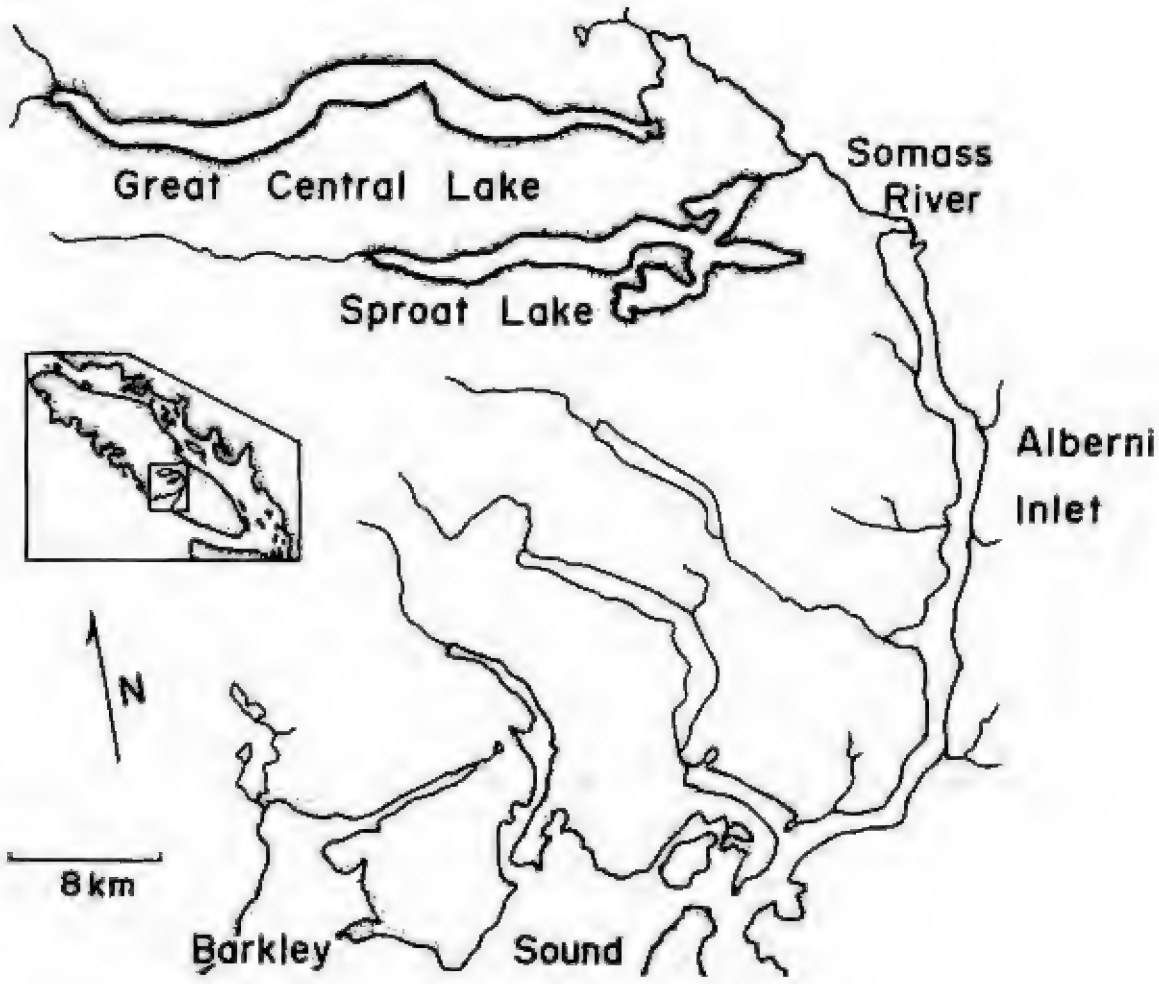

Figure 1
Map of Alberni Inlet, Vancouver Island, British Columbia, showing Sproat and Great Central Lakes.

the parasite can be readily identified in adult salmon, parasitological inspection allows an assessment of homing and straying between these two lakes. In Sproat Lake, 97.7% of the smolts were recorded as infected and 99.8% of the adults were infected (Table 1). This apparent increase in the infection rate is probably due to the fact that fish infected just prior to smolting do not yet carry the easily recognizable developmental stage (spores) and thus appear uninfected at that time, but are obviously infected as adults. Thus we can be quite certain that essentially no Great Central Lake (uninfected) sockeye stray into Sproat Lake.

While only 0.6% of the Great Central Lake smolts were infected, 5.2% of the returning adults were infected. This might be interpreted as evidence that some infected Sproat Lake salmon bypass their home river and enter Great Central Lake. However, recent experiments (Margolis, personal communication) have shown that sockeye smolts can acquire infective spores in the Somass River below Sproat Lake (Fig 1). Consequently, infected adults returning to Great Central Lake may have acquired the parasite as smolts in the Somass River and therefore may not represent strays from adjacent Sproat Lake. Thus there appears to be very little straying between adjacent Sproat and Great Central Lakes.

Another area where ***M. neurobius*** may be used to assess homing is the Smith Inlet–Rivers Inlet area of British Columbia (Fig 2). Sockeye salmon from Long Lake do not seem to be parasitized, but almost all from Owikeno Lake are infected (Table 2). Less data are currently available than there are for Sproat and Great Central

Table I

Occurrence of *Myxobulus neurobius* in the brains of sockeye salmon in the Barkley Sound, B.C., area. (L. Margolis, personal communication, 1984.)

Site/Year	Smolts # sampled	Smolts % infected	Adults # sampled	Adults % infected
		Great Central Lake		
1977	25	0.0	15	0.0
1978	100	0.0	245	0.8
1979	697	0.4	900	2.7
1980	460	0.9	1179	5.6
1981	506	0.0	1337	8.4
1982	250	0.4	4355	5.9
1983	574	1.2	1034	2.4
Total	2612	0.6	5389	5.2
		Sproat Lake		
1977	25	100.0	15	100.0
1978	54	96.3	175	99.4
1979	607	98.7	760	99.6
1980	431	97.0	1330	99.9
1981	475	97.3	1181	99.9
1982	297	99.3	843	99.9
1983	402	98.0	1127	99.7
Total	2291	97.7	5431	99.8

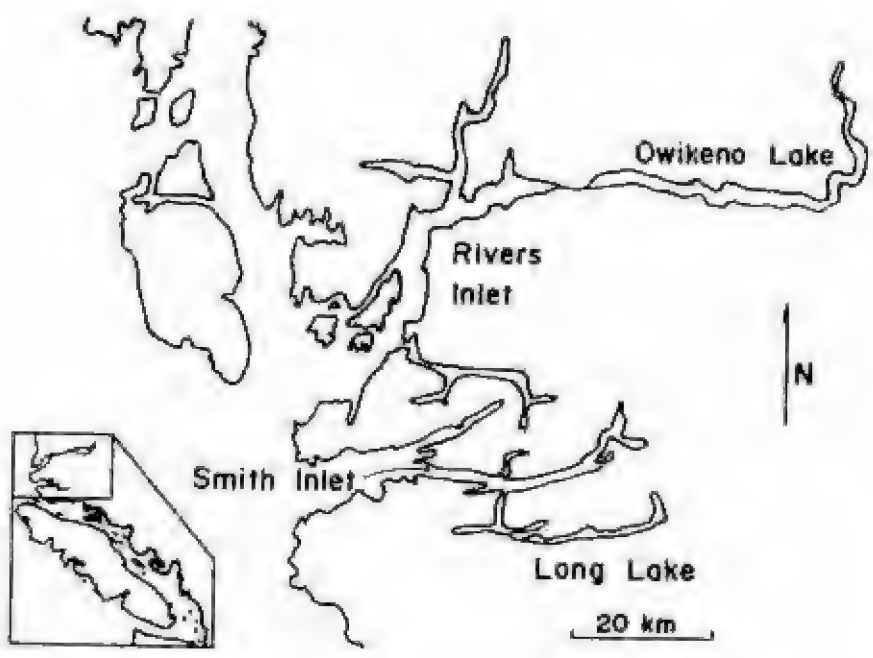

Figure 2

Map of Smith and Rivers Inlets, British Columbia, showing Long and Owikeno Lakes.

Lakes; nevertheless, there is no evidence that any Owikeno Lake fish stray to Long Lake. The Owikeno fish are not all infected, but this is not a priori evidence of straying from Long Lake since many lakes have infection rates of less than 100%.

The general conclusion that may be drawn from the parasitological data is that straying between these adjacent sockeye lakes is rare. Moreover, it is important to note that many sockeye populations are geographically isolated from conspecifics (Fulton 1970, Poe and Mathisen 1981). In such systems, straying is even less likely to occur than where other sockeye populations are nearby. Sockeye salmon tend to be concentrated in a few large populations, while other species of salmon may be found in more streams but are often less abundant. This is in large part due to the sockeye's virtual dependence on lakes for the first year or two of juvenile freshwater residency.

SPECIALIZATIONS OF SOCKEYE SALMON POPULATIONS

Sockeye salmon populations appear to have become highly specialized for the river-lake systems where they are reared and spawn (Ricker 1972). Carefully controlled studies have seldom been carried out, but racial differences have been reported in adult size, egg size, developmental rate, residual yolk at emergence, body weight of fry (Mead and Woodall 1968) and susceptibility to infection (Bower and Margolis 1984). Post-facto explanations for these differences are debatable, but it is interesting that Cultus Lake eggs are especially small (dry weight = 36 mg vs. 57 and 65 mg for Weaver Creek and Upper Pitt River sockeye, respectively (Mead and Woodall 1968)). Sockeye spawn on beaches in Cultus Lake, where dissolved oxygen levels can be as low as 3.0 $mg \cdot l^{-1}$ (Brannon 1965). The greater surface-to-volume ratio of small eggs might make them more viable at low oxygen levels. The period between egg deposition and fry emergence is very perilous, and mortality averages about 90% (Foerster 1968). Thus any specializations for the temperature or flow regime of the river, gravel size, or oxygen levels that increase survival will be favored.

Brannon (1967, 1972) also found racial differences in egg size and developmental rate, but of particular interest was his discovery that fry differed in rheotactic responses. Fry from a population that spawns above Fraser Lake in Stellako River had a strong downstream preference, whereas fry from a population spawning in the outlet of Chilko Lake had an upstream preference. Chilko-Stellako hybrids and fry from a beach-spawning population (Cultus Lake) displayed intermediate responses to water flow, indicating that rheotactic responses are adaptations to facilitate lake-finding behavior in these fish (Table 3). Similar results were also reported by Raleigh (1967, 1971).

The time when fry enter their nursery lake can be crucial to survival, as some lakes are oligotrophic with abrupt spring plankton blooms that support the sockeye. Goodlad, Gjernes and Brannon (1974) reviewed data on four lakes in the Fraser River system and concluded that fry entrance times were related to the seasonal patterns of temperature and zooplankton abundance in the lakes. Fry emergence timing is influenced by river temperature regime and developmental rate. There are racial

Table 2

The occurrence of *Myxobolous neurobius* in the brains of sockeye salmon from Long and Owikeno Lakes. (L. Margolis, personal communication, 1984.)

Site	Sample	Year	Number Sampled	Percent Infected
Long Lake	Smolts	1977	25	0.0
		1979	238	0.0
		1984	200	0.0
		Total	463	0.0
	Adults	1978	50	0.0
		1983	100	0.0
		Total	150	0.0
Owikeno Lake	Smolts	1978	300	88.7
		1979	205	79.2
		Total	505	84.7
	Adults	1978	269	98.1
		1979	380	96.8
		1983	150	100.0
		Total	799	97.9

Table 3

The rheotactic responses of newly emerged hatchery-reared sockeye salmon fry from Stellako River, a lake inlet; Chilko River, a lake outlet; Cultus Lake, where adult salmon spawn in the lake itself, and Stellako-Chilko hybrids. Fry were tested in groups of 100 (from Brannon 1967).

Stock	Number of tests	Percent upstream	Percent downstream	Percent not trapped
Stellako	20	15	80	5
Stellako-Chilko	20	48	48	4
Chilko	20	82	14	4
Cultus	15	57	36	7

differences in developmental rate, but the time when adult salmon spawn is the primary mechanism adjusting emergence time to meet the demands of particular lake-river systems. Brannon (1984) summarized evidence from many sockeye populations in the Fraser River system which indicated that spawning times maximize the subsequent temporal coincidence between fry emergence and the spring planktonic bloom in the lakes. Godin's (1982) review also concluded that the timing of emergence and migration is critical for survival in young salmon at these vulnerable stages, and that some genetic specialization seems to have occurred.

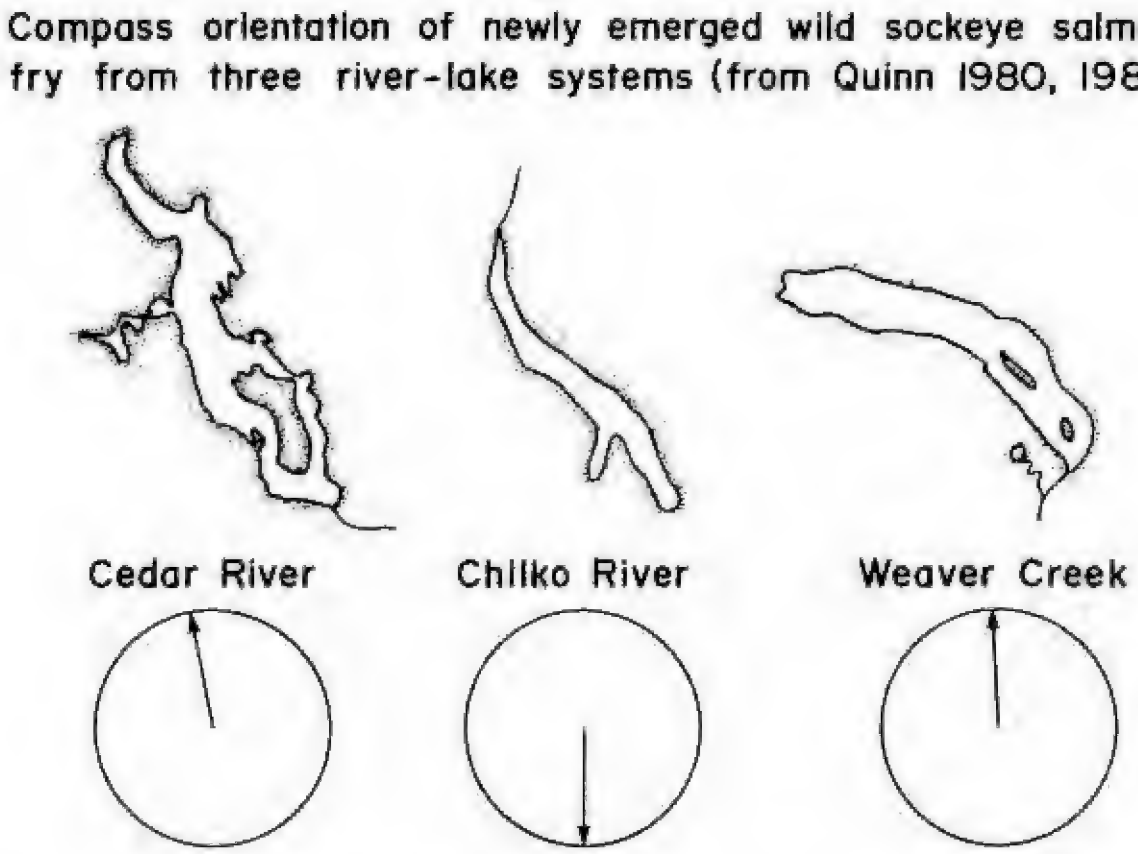
Compass orientation of newly emerged wild sockeye salmon fry from three river-lake systems (from Quinn 1980, 1982)
Cedar River
Chilko River
Weaver Creek

Figure 3

Mean compass bearings of newly emerged sockeye salmon fry from three populations: Cedar River–Lake Washington, Chilko River–Chilko Lake, and Weaver Creek–Harrison Lake (data from Quinn 1980, 1982a).

Adaptations of sockeye salmon for their egg incubation habitat and lakeward migration are under partial genetic control. Moreover, the dispersal migration of fry that reach the lake may also have a genetic component. Lakeward migrating fry tested in radially symmetrical arenas tend to swim in the compass direction appropriate for migration in that particular lake (Brannon 1972; Quinn 1980, 1982a; Brannon, Quinn, Lucchetti and Ross 1981) (Fig 3). After a year or two of lake residence, sockeye smolts must migrate to the lake's outlet prior to migration downstream to the ocean. In some cases the outlet area is unfamiliar to the fish, and evidence again indicates that stock-specific compass directional preferences may aid migration to the outlet (Groot 1965, Simpson 1979).

Leaving their nursery lakes, sockeye smolts migrate downstream and into the North Pacific Ocean. There is evidence that sockeye populations from Asia and North America have different but overlapping oceanic distributions, and that fish from Bristol Bay, Alaska do not entirely overlap with other North American populations (French, Bilton, Osako and Hartt 1976). However, the general pattern is that sockeye range widely on the high seas and mix with other populations and other species of salmon. The return of adult salmon to coastal waters from oceanic feeding areas is rapid and apparently well oriented (Royce, Smith and Hartt 1968; Quinn 1982b). Sockeye salmon destined for different rivers in the Fraser River system have a very well-established order in which they appear in coastal fisheries, spawn and die (Killick 1955). Brannon (1984) presented data on mean spawning dates and incubation temperatures for 17 sockeye spawning areas in the Fraser River system. Low

temperatures were correlated with early spawning, higher temperatures with late spawning (Spearman's Rank Coefficient $r_s = 0.96$, $p < 0.001$, $n = 17$, calculated from the data in Brannon's Figure 3). There have been no controlled studies of the genetic influence on spawning to date, but it is likely that this trait is at least partially a heritable specialization for the spawning-rearing systems.

THE EVOLUTION OF HOMING IN SOCKEYE SALMON

Since all present-day salmonids spawn in freshwater, it is generally believed that the ancestral salmonids were freshwater fish (Hoar 1976). Thorpe (1982) has challenged this view, arguing for marine ancestry. Our views on the origin of salmonids may affect how we envision the early evolution of homing, but this subject is beyond the scope of this paper. However it evolved, homing is clearly central to the life history of modern Pacific salmon. Populations specialize for the characteristics of the river where adults spawn, eggs incubate, and where juveniles reside. However, it has often been noted that homing can be a mixed blessing for two reasons: (1) it renders the population vulnerable to a natural disaster, and (2) it prevents colonization of new habitats (see comments by Hanamura 1966, Hasler 1966, Semko 1960). It has been reasoned that straying constitutes a form of genetic gambling: if egg-fry survival in the natal stream is very poor one year, members of the population that strayed might produce more offspring than those that homed that year (Quinn 1984). In stable rivers with high, predictable survival rates of eggs and juveniles, the average reproductive success of homing fish would be higher than that of strays, since they would be better adapted for their home river than for other rivers nearby. Suggestive evidence presented by McCart (1970) indicates that sockeye that spawn in unstable rivers may stray more than those in stable rivers. Moreover, Shapovalov and Taft (1954) reported high levels of straying by coho salmon (*O. kisutch*) in two very unstable coastal streams. Theoretical analysis by Roff (1975) indicated that environmental heterogeneity can affect the selective advantage of dispersal (i.e., straying). However, a model by Hamilton and May (1977) revealed that adaptations for dispersal can be important even in highly predictable environments.

Besides the stability of the spawning stream, its similarity to adjacent streams may influence straying. Adjacent sockeye systems are often very different from each other, but the short coastal streams used by many populations of pink (*O. gorbuscha*), chum (*O. keta*) and coho salmon may be quite similar in temperature and flow regime. In such cases, adaptations for the home stream would not seriously disadvantage a straying fish.

Regardless of whether they spawn in their home stream or elsewhere, salmon commit their lifetime reproductive output to one season's spawning (unlike the iteroparous trout *Salmo* spp. and char *Salvelinus* spp.). However, if the progeny of a given salmon return at different ages, there may be a greater chance that at least one of these age classes will spawn under favorable conditions than if all returned to spawn in the same year. Thus age class variation constitutes a form of temporal

straying. Species with little variation in age at maturity might balance this lack of straying in time with relatively more spatial straying. However, variation in age at maturity is an evolved characteristic, not an ecological pressure in the sense that stream stability and uniqueness are. Presumably, various factors influence age at maturity.

In the foregoing discussion, three factors have been identified as potentially important in the development of homing/straying behavior in salmon species and populations: (1) the stability of the spawning area as determined by survival to seaward migration, (2) the complexity of the spawning stream and its difference from adjacent streams, and (3) variation in age at maturity. While salmon populations vary considerably, the relative amounts of homing and straying in the five North American species of Pacific salmon may be predicted according to these criteria (Table 4). At present, too little data are available to rigorously test these ideas, but the high degree of homing predicted for sockeye salmon seems to be borne out. Moreover, the high degree of homing predicted for chinook salmon (Table 4) is supported by recent data on spring chinook returning to the Cowlitz River Hatchery, Washington (Quinn and Fresh 1984).

Spawning stream selection has been discussed as though the fish are genetically programmed to home or stray, regardless of the sensory or physical requirements for homing. There are undoubtedly many proximate factors that influence straying. For example, if access to the natal stream is blocked, salmon will enter and spawn in other rivers. Degradation of the spawning river may influence straying (IPSFC 1965; Whitman, Quinn and Brannon 1982). In addition, some rivers may be more difficult to identify than others on the basis of their chemistry. The choice of spawning stream may also be influenced by pheromones, as adult salmon are attracted to the chemical traces of conspecific adults (Pete 1977) and juveniles (Quinn, Brannon and Whitman 1983). However, the existence of such proximate influences on spawning stream selection does not mean that there cannot also be a heritable tendency to stray.

Life-history theory has been applied to the patterns of age at first reproduction in Atlantic salmon *Salmo salar* (Schaffer and Elson 1975) and to the relative advantages of iteroparity and semelparity in salmon (Schaffer 1979) and American shad *Alosa sapidissima* (Leggett and Carscadden 1978). Straying and homing may also be life history patterns with probabilistic advantages and disadvantages to individual fish. However, homing and straying are not viewed as evolutionarily stable strategies (ESSs) as defined by Maynard Smith and Price (1973). Under most conditions, the average reproductive success of homing (locally adapted) fish will exceed that of strays. Periodic catastrophes that reduce the population of homing fish give the strays temporary advantage. In an extreme case, the 18 May 1980 eruption of Mt. St. Helens devastated the Toutle River in Washington State. The combination of heat, ash, mud and flooding almost certainly killed all the juvenile salmon in the river. If so, the only Toutle River coho salmon that spawned in 1979 that left any offspring were those that strayed. Moreover, the re-population of the river will also be by strays.

Table 4

Hypothesized variation in straying tendencies in Pacific salmon, based on three factors which may affect homing. Salmon species are ranked according to general spawning stream characteristics and life history, but substantial variation among populations exists. Stream stability, complexity, and age class variation decrease from left to right.

	Predicted Level of Homing
Stream stability	Chinook > Sockeye > Coho > Chum = Pink
Stream complexity	Sockeye > Chinook = Coho > Chum = Pink
Age class variation	Chinook > Sockeye = Chum > Coho > Pink

The choice of spawning streams influences the inclusive fitness of individual salmon, but homing and straying patterns also determine the distribution of the species. Much of the area presently occupied by North American salmon was covered by the Cordilleran ice sheet during the Wisconsin glacial period, between about 50,000 and 10,000 years ago. During this period, it is generally believed that salmon existed in the Bering refuge (unglaciated regions of Alaska, the Yukon Territory, St. Lawrence Island and adjacent parts of Siberia) and the Pacific refuge (the Pacific watershed south of the Cordilleran ice sheet, including the Columbia and Sacramento Rivers) (McPhail and Lindsey 1970). Virtually all the present range of sockeye salmon in British Columbia, including the many important tributaries of the Fraser River, were uninhabitable as little as 10,000 years ago. This means that the colonization of rivers as far as 1152 km inland (Forfar Creek) and 1170 m in elevation (Chilko River), and the attendant specializations occurred in some 2500 generations. By definition this colonization was not accomplished by homing but by straying. Withler (1982) recently reviewed the history of Pacific salmon transplants and noted that there are only a few examples of successful introductions to barren rivers within the range of salmon. He concluded that virtually all suitable, accessible spawning areas are currently being used by salmon. Most range extensions occur when a physical barrier to upstream movement is removed, as was the case when sockeye salmon were established in Frazer Lake, Alaska in the 1960's. When salmon are transplanted outside their natural range, they perish if the environment is not suitable, but they can spread rapidly under favorable conditions. The colonization of the Great Lakes by pink salmon following release of only 21,000 juveniles into Lake Superior in 1956 testifies that a great deal of successful straying occurred (Kwain and Lawrie 1981).

SUMMARY

More evidence is needed to document the extent to which different populations and species of salmon return to spawn in their natal stream or stray and spawn elsewhere. Examination of limited data indicates that straying is rare in sockeye salmon. Compared to other species, sockeye populations tend to be isolated and quite specialized for their freshwater environments. This is consistent with high levels of homing. Three factors may determine the relative degree of selection for homing and straying: the stability of the freshwater spawning and rearing area, the area's complexity and difference from adjacent areas, and the variation in age at maturity. Since the five species of North American Pacific salmon vary in these characteristics, we can make predictions regarding their relative homing tendencies. Data on homing acquired in the future may thus be used to test these predictions. Finally, while the choice of spawning stream is vital to individual fish, it is also important in establishing and maintaining the distribution of the species. Since much of the present range of Pacific salmon was glaciated until about 10,000 years ago, colonization by straying has occurred often and with great significance for salmon.

ACKNOWLEDGMENTS

I am grateful to Dr. Ernest Brannon for introducing me to sockeye salmon several years ago, and to him and Dr. Cornelis Groot for countless discussions on various aspects of salmon homing and life history. Dr. Leo Margolis provided the unpublished parasitological data and information needed to interpret it. I am also very grateful to Dr. Mart Gross for valuable discussions and to Sherry Greenham for drawing the figures.

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CHAPTER FOUR

TERRESTRIAL VERTEBRATES

The arena of terrestrial migration turns out for this symposium to be represented by a collection of otherwise neglected taxa. Except for phytoplankton, plants have generally been excluded from consideration. I suppose the topic of migration and dispersal in animals seems already complex enough without getting encumbered in pollination mechanisms, seed dispersal and the like. Birds and insects are covered extensively in sessions of their own, as is amply justified by the major advances that investigators with these taxa have contributed to the subject. One other major terrestrial group not covered in this symposium but for which important data on dispersal exist is the arachnids. I am sure that much of interest resides with this group, but it could not be accommodated here. This leaves for us mammals, including the quasi-terrestrial bats, reptiles, and amphibians. An assemblage of leftovers, perhaps, but for the subject before us and for understanding our own species, they are of critical importance.

Having determined that the boundaries of my subject encompassed tetrapod vertebrates minus birds, I next had to decide whether to approach the subject by taxa or along functional lines. My preference was the latter, since this was to be a symposium whose major objective was to foster communication among workers using diverse organisms. Would it not be ideal to find speakers who would review, across terrestrial vertebrates, such topics as navigation, demographic features, evolutionary issues, true (round-trip) migration versus dispersal, behavioral aspects, and physiological substrates?

Unfortunately, this idea was quickly abandoned when I realized that most researchers in this field are taxon-oriented. It would be a test of the success of this symposium in enhancing communication to see if future symposia could be organized functionally.

Four of the five speakers were chosen to represent key taxa. Ross Kiester (Tulane University) is an authority on dispersal in amphibians and reptiles, groups which have been relatively little-studied in this regard. Marine turtles of course are known for their spectacular migrations to egg-laying beaches, but technically are outside the limits of this terrestrially-oriented session. Kiester's own work on box turtles is destined to be a classic for this group of vertebrates. Brock Fenton (Carlton University) has had extensive research experience with various aspects of bat biology. He summarizes here information on dispersal and migration in this extremely diverse group of mammals. Other than birds, bats represent the one tetrapod group in which studies of navigation have been an important aspect. Dale McCullough (University of

California, Berkeley) reviews movements in large mammals, primarily ungulates. His own research has concerned the population and social dynamics of a variety of ungulate species, and he has an impressive overview of this group. My own review on dispersal in small mammals mainly concerns rodents. Rodents are the most speciose of the living mammalian orders and have figured importantly in basic research on ecology and behavior. Because of their size and numbers, small mammals are especially suited for ecological and genetical investigations.

As extensive as is the coverage by these speakers, several major mammalian groups remain neglected. Of most importance to this field are the primates and marine mammals. Both of these groups would justify a symposium session for themselves. The latter of course are not terrestrial, and we can excuse their omission on those grounds. The final speaker, Robin Baker (University of Manchester) has had extensive experience with a variety of mammalian groups, including primates. His contribution thus serves to some extent to fill this taxonomic gap. But, more importantly, he attempts to generalize principles of navigation across vertebrates, including humans. His research has often been controversial, but all can agree that it is both synthetic and stimulating. The invited speakers were supplemented with a fine series of seven contributed papers and posters. Three of these are represented by contributions to this volume.

I would like to express my appreciation for the enthusiastic cooperation of all the speakers; it has been a pleasure working with them. And, finally I offer my gratitude to Mary Ann Rankin who invited me to participate in what was for me a productive, stimulating and enjoyable conference.

William Z. Lidicker, Jr.

AN OVERVIEW OF DISPERSAL IN NON-VOLANT SMALL MAMMALS

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ABSTRACT

Early views of dispersal as being equivalent to mortality and occurring only from saturated habitats have changed with an appreciation that dispersal can occur at densities below carrying capacity (pre-saturation dispersal) and can involve both sexes, multiple ages and be seasonally correlated. Current thinking incorporates habitat patchiness and population structuring into this complex. The demographic implications of dispersal have been extensively explored in small mammal populations and found to be profound. Effects on population growth rates, sex ratios, age structure, and social conditions can be anticipated. To explore the potential role of dispersal in population density regulation, two hypotheses for explaining the multi-annual cycles often seen in microtine rodents which involve dispersal as a major component are reviewed. One (Chitty-Krebs) involves a dispersal polymorphism and the other pre-saturation dispersal combined with habitat patchiness.

Emphasis is placed on the heterogeneous nature of movements beyond the boundaries of home ranges, and a heuristic classification of dispersal types is suggested. Aside from nomadism, exploratory excursions and true migration, five kinds of dispersal are postulated. Motivations for dispersal and the characterization of dispersers with respect to sex, age, behavior, condition, and genetics are closely linked and of course vary with dispersal type. Some future directions for research are suggested.

INTRODUCTION

While species of non-volant, small-sized mammals are generally less spectacular and of less economic benefit than typical large-sized mammals, colorful birds, fish, lobsters, or butterflies, it is the thesis of this paper that studies on small mammals (less than 5 kg in body weight) have contributed and will continue to contribute in major ways to dispersal theory. Such contributions have been primarily in the areas of ecology and evolution with much less being offered to our understanding of navigation and the physiological and behavioral substrates of dispersal movements. Some redress of this imbalance seems likely in the future.

The process that we wish to understand is the leaving home, travel, and re-establishment in the new home that is such a common phenomenon among organisms. Even permanently sessile creatures achieve dispersal by using propagules or mobile gametes. Small mammals are not sessile and often move their home several times during their lifetimes. True migration (round-trip) is known to occur in only a few species of small mammals, and so has not been a major focus of research with this group of organisms. Rather, attention has been focused on the amount and timing of movements, their motivation, and their demographic and genetic consequences. One of the critically important results of this effort is the realization that dispersal often is not a simple nor homogeneous phenomenon even within a particular species. Understanding therefore requires an appreciation of this complexity and heterogeneity.

In this contribution, I will comment on the historical progression of views about dispersal in small mammals and on what is known about the demographic implications of such movements, attempt to outline a classification of dispersal, indicate the relation between the nature of dispersers and the kind of dispersal in which they participate, and finally, suggest some possibly productive directions for future research.

HISTORICAL PROGRESSIONS

It was the classical view among small mammal ecologists, as well as that of ecologists in general, that dispersal was appropriately considered a component of "gross mortality" (Lidicker 1975). Perhaps it could be admitted that an occasional disperser achieved spectacular success, but generally whether a disappearing individual died or dispersed mattered not at all. The consequences for the source population and for the individual were identical. Besides, it was terribly difficult in practice to distinguish these two kinds of losses. Concordant with this view was the notion that individuals only left home under desperate circumstances. An individual's home must be economically or socially untenable to justify the risks of almost certain death to the disperser. Only the spectacular seasonal migrations, known for many temperate and Arctic species, were considered to have adaptive significance. From our current perspective, it is hard to believe that such a naive view was so generally acceptable. For further comments on this early attitude, see Lidicker (1975) and Lidicker and Caldwell (1982: pp. 1–2, 202).

In the last several decades it has become unavoidably apparent that most dispersal actually occurs when conditions are not desperate for the disperser. That is, dispersal actually occurs routinely by particular sex or age groups, at certain seasons of the year, and during low and increasing population densities. I labeled this common sort of dispersal "pre-saturation" (Lidicker 1975) to contrast it with the classical "saturation" type which occurs when habitats are filled to capacity. Pre-saturation dispersal is therefore defined as dispersal occurring when the carrying capacity of the habitat has not been reached (see Fig 1). Carrying capacity for this purpose is measured in terms of essential economic resources such as food, water, and shelter (Lidicker 1978, pp. 126–127).

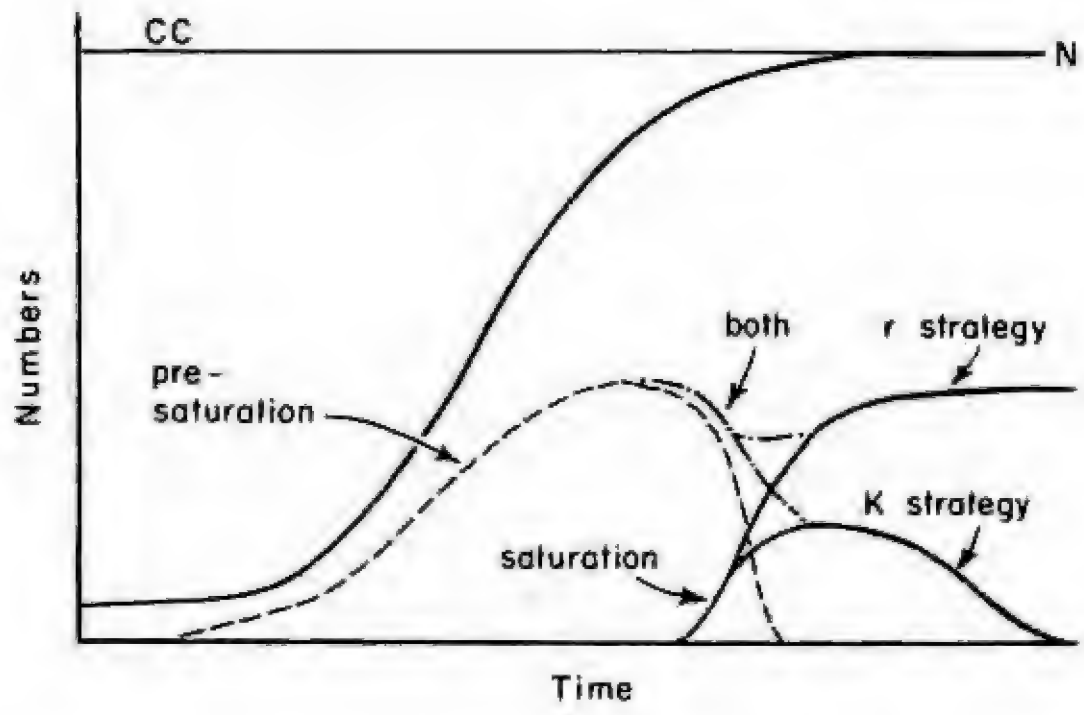

Figure 1

Saturation and pre-saturation dispersal (and both combined) as a function of population numbers (*N*) and carrying capacity (*CC*) of the habitat. The level of saturation dispersal will vary depending on whether equilibrium densities are achieved primarily by increases in mortality rates (*r*-strategy) or decreases in natality rates (*K*-strategy). The nature of dispersal from declining populations (not shown) will depend on whether or not a falling carrying capacity is responsible for the decline.

The recognition of pre-saturation dispersal carries profound implications for the ecological and evolutionary consequences of dispersal movements. Not only is the timing and quantity of dispersal strongly influenced, but the nature of the dispersers themselves is expected to be fundamentally different. Unfortunately, we still have very little direct evidence for the qualitative nature of dispersers under these two strikingly different conditions. We can, however, predict the following. Saturation dispersers, constituting surplus individuals from saturated habitat, will generally be those in poorest condition to compete for limited resources. These will be those in poor health, juveniles, the very old, and otherwise socially subordinate individuals. We can presume that such individuals are least likely to be successful when faced with the harsh realities of being a disperser. See Lidicker and Caldwell (1982, Part III) for a review of the hazards accruing to dispersers. Pre-saturation dispersers will represent quite a different collection of individuals. These dispersers will be in relatively good condition, having left home when resources were not in overall short supply. They may represent a random cross-section (rank-order template) of the source population or some genetically prescribed age or sex cohort. Such individuals can be expected to have a much greater chance of surviving and re-establishing elsewhere than do saturation dispersers. Because of this presumed difference in average success rates, it is pre-saturation dispersal that is likely to be favored and molded by natural selection. For further development of this point, see comments and references in Lidicker and Caldwell (1982, Part V).

Current thinking about dispersal incorporates the rapidly expanding knowledge that we have about the patchiness of species distributions. Rather than an assumed generality, it now appears to be a rarity for species to exhibit fairly homogeneous distributions across the landscape. With patchiness comes the question of movements among patches. Hence dispersal is the glue that ties the ecological, genetic and behavioral parts of modern population biology together. It has also become an essential ingredient in wildlife management and in the design of nature reserves. Thus what was only a few years ago a "humdrum process" (Elton 1927, p. 148), largely neglected by biologists, has become an integral part of research on life history strategies, population dynamics, evolutionary processes, and resource management.

DEMOGRAPHIC IMPLICATIONS

Once dispersal became appreciated for its generality and impressive magnitude, demographic causes and consequences of this behavior soon became apparent. These have been reviewed for small mammals by Lidicker (1975), Gaines and McClenaghan (1980), Tamarin (1980), and Stenseth (1983), and for the extensively studied voles (meadow mice), genus ***Microtus***, by Lidicker (1985).

The demographic effects of dispersal are predicated upon: (a) the quantity of dispersal and its timing, (b) the possibility that dispersers are a nonrandom subset of residents, (c) the success rate of dispersers in establishing new home sites, and (d) the spatial structuring of populations among which dispersers move. Little is known about the success rate of dispersers, but we can presume that pre-saturation dispersers will have much higher average success records than will saturation dispersers. Also some data are available on the abilities of a few species to cross water barriers (for review, see Carter and Merritt 1981).

It seems generally to be the case in small mammals that dispersal is nonrandom with respect to age, sex, and reproductive state relative to residents. Two well-documented exceptions are the cotton rat ***Sigmodon hispidus*** (Joule and Cameron 1974, Stout and Demmer 1982, Stafford and Stout 1983) and the beach vole ***Microtus breweri*** (Tamarin 1977). Where dispersal is differential, the possibility is opened for effects on age structure, sex ratio, and reproductive state of the resident population. Such populations will be diminished by whatever class of individuals is over-represented among dispersers. Likewise, populations composed largely of immigrants will be characterized by traits which dominate among dispersers. A growing number of examples are available to support this class of phenomena (see reviews cited above).

It is the quantitative and timing aspects of dispersal that have so far received the most attention. A close relationship between dispersal and population density can be predicted both because dispersal is likely motivated by deteriorating economic and social conditions, and because, where dispersal takes the form of emigration and immigration, it becomes part of the basic growth equation. Population growth rates can be equated to birth rates plus immigration rates diminished by death rates plus emigration rates. A suppressing effect on population growth rates can therefore be

expected where there is a positive net emigration rate and densities are below carrying capacity. Perhaps the best-documented example of this among small mammals is the California vole ***Microtus californicus*** (Lidicker 1975, 1980; see Fig 2). Similarly, immigration can enhance growth rates (note, for example, that the annual population growth rate for the United States is approximately double what it would be based on births and deaths alone).

Gaines and McClenaghan (1980) have reviewed the literature on dispersal and density and conclude that: (1) the number of dispersers tends to be positively correlated with density, (2) a less consistent positive relationship is found between numbers of dispersers and rates of population increase, and (3) more dispersal consistently occurs during periods of increasing density than during phases of decline. Overall, they feel that dispersal rates are density independent. Stenseth (1983) proposes a model in which dispersal will be maximal when population growth rates are maximal, dropping off again as density approaches asymptotic levels. This generally supports Gaines and McClenaghan's conclusions but would further weaken any positive correlation between numbers of dispersers and population growth rates. Neither summary adequately accounts for phases of stable or declining densities. According to the graphical model shown in Figure 1, dispersal rates at such times will vary greatly among different species but generally will be much lower than at comparable densities during increase phases, especially during declines (not shown in the figure). Any consistent relationship between density and dispersal is not likely, therefore, unless phase of population growth is considered. On the other hand, Joule and Cameron (1975) claim that dispersal is consistently and positively correlated with density in both ***Sigmodon hispidus*** and ***Reithrodontomys fulvescens***.

The fourth variable in considering the demographic aspect of dispersal is that of spatial structuring of populations. By spatial sructuring, I refer to the uneven dispersion of individuals that generally characterizes small mammal populations. Interest in the ecological implications of such uneven distributions over space has been expanding rapidly in recent years. Clearly, dispersal is the process by which subpopulations are variously connected. Individuals, genes, and even information are exchanged in this way. If there is zero exchange, each subpopulation becomes an independent unit demographically and genetically. If exchange is rampant, the subpopulations effectively merge into a single functional unit. The interesting and difficult cases are the vast majority lying in between these two extremes.

We are now poised for a consideration of the important question of the potential role of dispersal in the regulation of population density. This topic has been reviewed by Lidicker (1975), Krebs (1978b) and Tamarin (1980). In principle, dispersal could serve as a regulating factor for population growth if net losses to emigration increased proportionately as density increased. The critical time for this relationship would be just below or above density equilibrium levels. Several levels of involvement by dispersal in density regulation as well as several models for how dispersal could act as a regulating factor are described in Lidicker (1975).

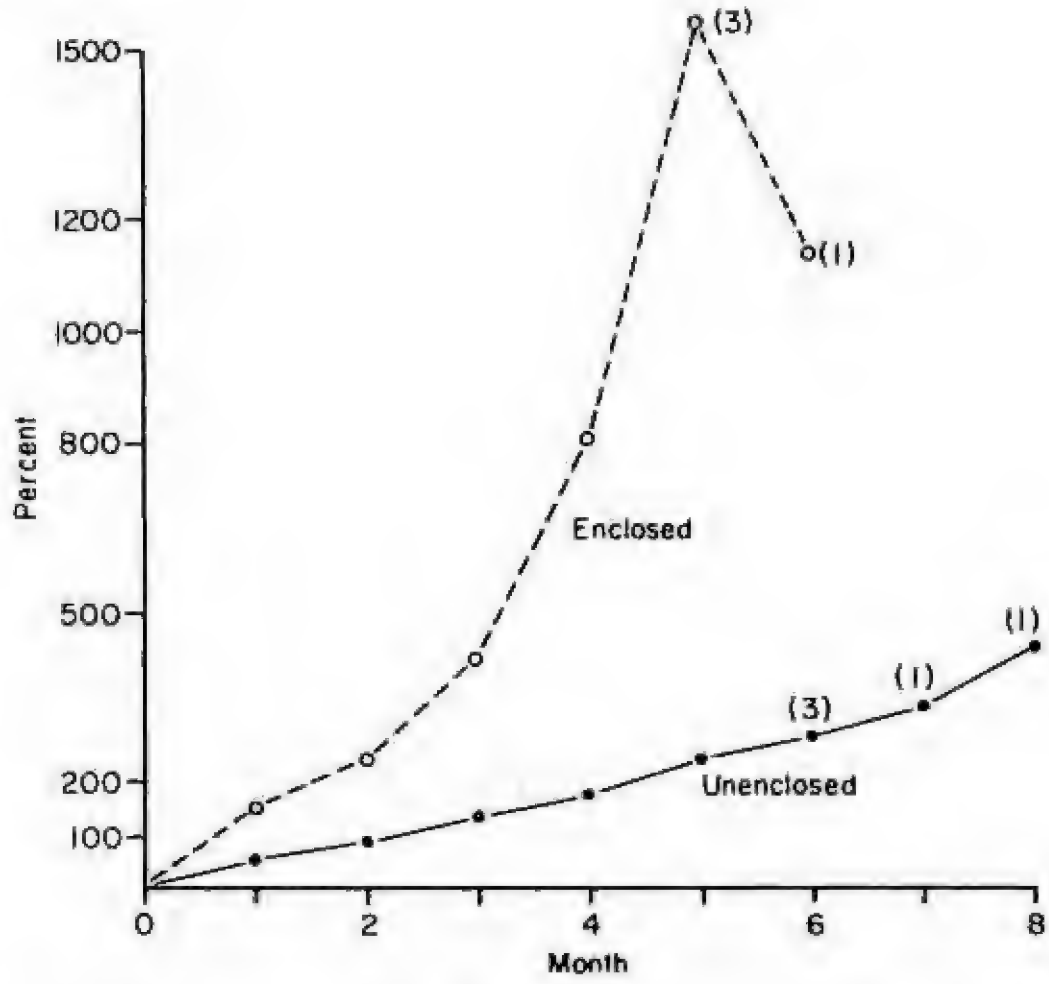

Figure 2

A comparison of population growth rates with and without emigration. Mean percentage increases in density (monthly intervals) from starting densities during periods of rapid population growth are shown for *Microtus californicus*. The dashed line represents four enclosed populations (enclosures or islands) and the solid line four unenclosed ones. Sample sizes below 4 are shown in parentheses. Data are from same sources as Figure 5.2 in Lidicker (1975). There is no overlap after month two in the values for the two classes of populations. (Reprinted from *The Biologist* 65: 51, 1980).

The role of dispersal in population regulation has been pursued most vigorously in attempts to model the multi-annual cycles commonly exhibited by species of microtine rodents. These enigmatic fluctuations show a two- to five-year periodicity, and have been the subject of intensive research for at least 50 years (for recent review see Krebs and Myers 1974). Two recent models invoke dispersal as a critical component of the cycle determining mechanism. The first of these is the Chitty-Krebs model named after its two principal architects (Krebs 1978a). It postulates a genetic polymorphism for dispersal behavior. At low densities a nonaggressive dispersal morph is favored. As density increases, the other morph which is aggressive and nondispersive is favored. It progressively drives the dispersal morph into marginal habitats. At peak densities, populations are composed largely of the aggressive morph which also has lower fecundity and is less able to cope with adverse conditions. When the next harsh season comes (usually winter), the population crashes to low numbers. Conditions again become favorable for the dispersal-type, and an increase phase again ensues. Thus the multi-annual cycle derives its primary mechanism from alternating selective pressures on these two behavioral morphs. Criticisms of this model have focused on: (1) its lack of connection to the nonsocial environment of the voles, (2) the need to invoke extremely strong selective pressures in order to cause

major shifts in gene frequencies over relatively short periods of time, and (3) the need to explain the extremely variable form and periodicity of fluctuations observed among different species of microtines and also often among different populations of the same species. Other criticisms as well as some support can be mustered.

The second model involves interactions between dispersal and micro-spatial structuring of populations and is outlined in Lidicker (1985, in press). It requires pre-saturation dispersal and the periodic development of large amounts of frustrated dispersal. When an individual is motivated to disperse but is prevented from doing so by physical, biotic or social barriers, it becomes a frustrated disperser (Lidicker 1975, pp. 117–120). The accumulation of such individuals in a population can have profound demographic effects. Such high levels of frustration typically occur on small islands or in artificially fenced populations but also occur periodically in unenclosed populations (as will be developed below). The result of such circumstances is a dramatic increase in densities, often followed by a severe crash or even extinction. This so-called "fence effect" is known for at least six species of ***Microtus*** (Lidicker 1984). The implication is that pre-saturation dispersal ordinarily keeps densities from increasing to such high levels that a massive decline follows.

This scenario is incorporated in my model for the multi-annual microtine cycle. This model has the additional feature of requiring a spatially sub-structured population. Considerable attention has been directed in recent years toward connecting multi-annual cycles in microtines to micro-spatial structuring of populations (Abramsky and VanDyne 1980; Anderson 1980; Bowen 1982; Charnov and Finerty 1980; Cockburn and Lidicker 1983; Hansson 1977; Hestbeck 1982; Mackin-Rogalska 1979; Rosenzweig and Abramsky 1980; Stenseth 1977, 1983; Stenseth, Hansson and Myllymäki 1977). These papers emphasize both the ubiquitous nature of patchy distributions, their association with multi-annual cycles, and the differential performance of voles in different quality patches. For my model only two classes of patch quality need to be distinguished. "Survival habitat" refers to patches in which survival is generally possible on a year-round basis, and reproduction is regularly supported during the appropriate breeding season. "Colonizing habitat" is excellent habitat for parts of an annual cycle and supports breeding during favorable times. However, it does not permit survival over the harshest seasons (winter or dry season) in most years, and in especially poor years reproduction may not be successful.

Some aspects of my model are shown schematically in Figure 3. Following a population crash, survivors are sequestered in survival habitat. During the first year (year 2 in Fig 3), reproduction is partitioned into modest growth within the survival patches and dispersal to uninhabited other patches. By the second year (year 3 in Fig 3) dispersers are moving out extensively into colonizing habitat. Growth in density is limited by the availability of extensive "dispersal sinks" (see Lidicker 1975). If such a breeding season is followed by a relatively favorable nonbreeding period such that survival of voles is extensive in the colonizing habitat, the population is poised to reach peak densities in the following year. If survival is poor in the colonizing habitat, the development of peak numbers will be postponed. In the peak year, dispersal sinks are quickly filled leading to massive frustrated dispersal and very

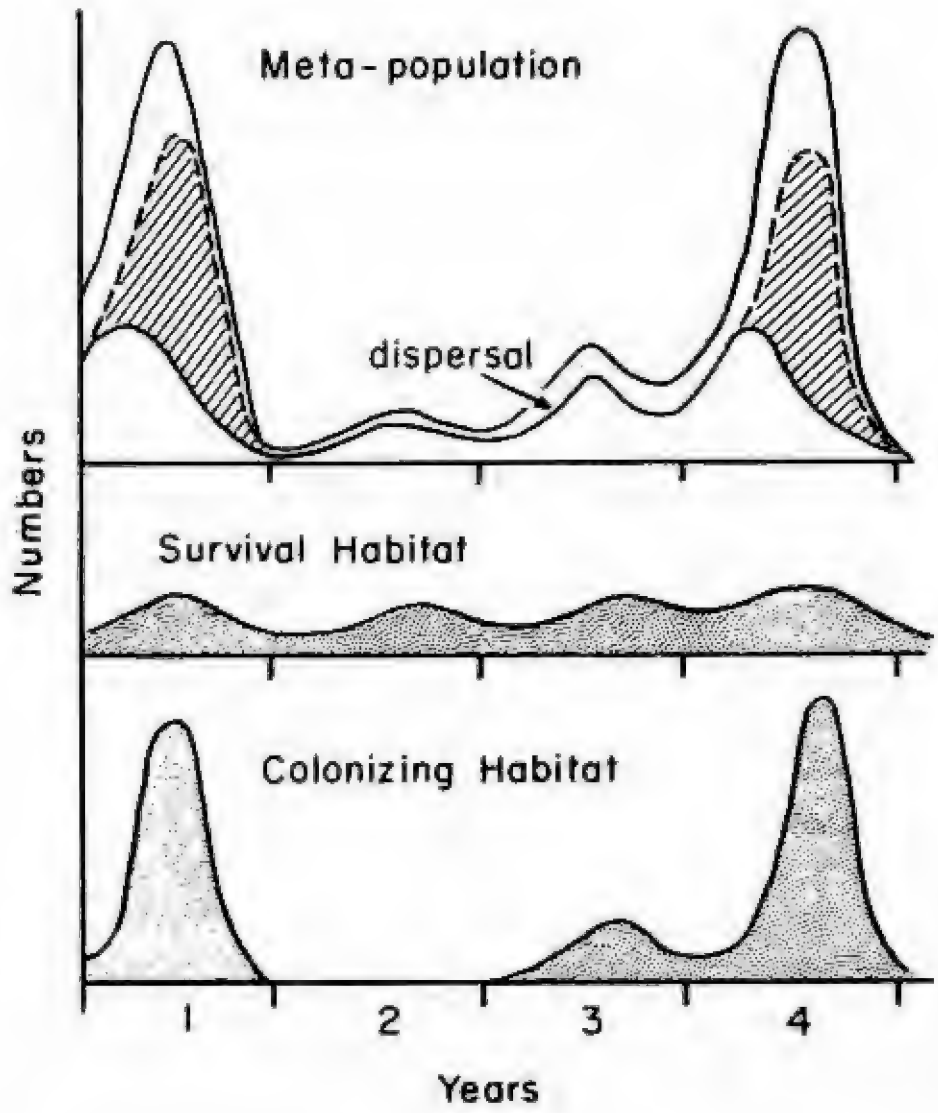

Figure 3

Model of population size and dispersal changes over an idealized microtine multi-annual cycle. Numbers are shown for the relatively rare patches of survival habitat, the abundant colonizing habitat and both combined (meta-population). The proportion of the population involved in dispersal movements is shown by the solid line under the meta-population numbers. Dashed lines encompassing hatched areas indicate the extent of frustrated dispersal.

rapidly growing numbers. Individuals presumably become "aware" of filled sinks through exploratory excursions and increased immigration pressures. Physiological and behavioral consequences of the frustrated dispersal, plus resource depletion and other factors, leads to a population crash. This is a multi-factorial model (Lidicker 1978), and this brief description does not include a number of other critical factors included in the regulation machinery. For our purposes here, the important ingredient is the spatial substructuring with the further proviso that availability of survival habitat patches is small relative to colonizing habitat. This stipulation is needed to insure that numbers are periodically brought to extremely low levels. If survival habitat is too abundant, harsh season numbers will not be depressed to a level that will prevent peak densities being reached on an annual basis. Some populations of microtines show this annual pattern (Lidicker 1973, Tamarin 1977).

Finally, it should be mentioned that there are circumstances in which pre-saturation dispersal alone can prevent the development of multi-annual cycles. This is the circumstance when a small survival patch is surrounded by a permanent dispersal sink. Abramsky and Tracy (1979) provide an example of this in their studies of

Microtus ochrogaster living in artificially fertilized and watered plots surrounded by short-grass prairie. Such prairie is relatively poor habitat but provides a continuously available dispersal sink, and this dispersal prevents high densities from developing in the favorable patches.

A CLASSIFICATION OF MOVEMENTS

One of the strongest messages to emerge in recent years from studies on dispersal in small mammals is that it is a heterogeneous phenomenon. In retrospect, this is hardly surprising. No one would expect that phenomena like mortality and natality would be simple and homogeneous processes in natural populations. Just as these major classes of demographic processes can have multiple causes and consequences, so too will dispersal have a variety of motivations, timings and consequences. It is critical that this heterogeneity be acknowledged before our understanding of dispersal can be substantially improved.

The following classification attempts to define those movements which organisms make outside of their normal home ranges (Table 1). Deliberately excluded are the ordinary movements engaged in during daily activity patterns within established home ranges. Thus the single unifying behavior for the movements considered here is that an organism leaves its home range. If it also leaves the population under study, it can be said to have emigrated. Similarly, individuals entering a population of which they are not members are immigrants. This tentative classification is derived from studies on small mammals, but should be more generally applicable.

Nondispersal Movements

First to be considered are two kinds of movements not ordinarily considered to be dispersal. These are ***nomadism*** in which no home range is established, and ***excursions***. Exploratory excursions are probably common among small mammal species. Individuals leave their home range for a short period of time (few days or less) and then return home. Such trips may represent incipient dispersal, or they may be attempts by either sex to find mates. Of course if an individual fails to return from such an excursion for whatever reason, it automatically becomes a dispersal event. Excursion data for ***Peromyscus*** are summarized by Stickel (1968, pp. 398–399). Madison (1980a,b) claims that such trips are common in ***Microtus pennsylvanicus***. Based on homing data (Fisler 1962), this is likely true also for ***M. californicus***, and Saitoh (1983) documents age and sex variations in excursions in ***Clethrionomys rufocanus***. Shillito (1963) concludes that in the laboratory, reconnaissance behavior in ***M. agrestis*** is both instinctive and regularly occurring. As techniques improve for following the details of individual movements (such as radio-telemetry), many more examples will undoubtedly be reported.

Table 1
A classification of extra-home range movements.

A. Nondispersal	B. Dispersal
1. Nomadism	1. Migration
2. Excursions	2. Saturation
	3. Pre-saturation
	a. Seasonal
	b. Ontogenetic
	c. Colonizing
	d. Interference

Dispersal Movements

True dispersal occurs whenever an organism leaves home either permanently or at least for a long period of time. A special class of dispersal is ***migration***. Among vertebrate biologists this term is usually restricted to movements which have both going and coming back components. They are thus like excursions, but are long-term. Usually they are organized seasonally and involve fairly synchronous movements by entire populations. Such migratory movements have not often been described for species of small mammals. Perhaps best known are seasonal habitat shifts indulged in by lemmings (***Lemmus***). These data are summarized by Stenseth (1983). Small-scale movements of the same type have also been recently reported for both ***Lemmus*** and ***Dicrostonyx*** on the Alaskan tundra by Batzli, Pitelka and Cameron (1983). Storer, Evans and Palmer (1944) have described seasonal migrations by ***Peromyscus boylii*** in the Sierra Nevada of California, and Tast (1966) reports on the regular seasonal movements of ***Microtus oeconomus*** into and out of river flood plains. A similar pattern has been described for several species of rodents and shrews inhabiting the Kafue River Flats of Zambia (Sheppe and Osborne 1971, Sheppe 1972). It seems likely that migratory movements are more widespread among species of small mammals than these few examples would indicate. Obviously, the detection of migration is more difficult for small cryptic species than it is for those more easily observed.

Nonmigratory dispersal is the ubiquitous and quantitatively important behavior of small mammals. The following categories of dispersal represent a first attempt to organize our thinking about this complex of behaviors. No attempt is made to review exhaustively the extensive literature on this subject. Recent reviews have been provided by Gaines and McClenaghan (1980) and Stenseth (1983), and I have recently summarized available information on North American members of the genus ***Microtus*** (Lidicker 1985b).

The concepts of ***saturation*** and ***pre-saturation dispersal*** have already been defined. As these are based on when dispersal occurs relative to how population density relates to the carrying capacity of the habitat, both categories can be usefully subdivided on the basis of other criteria. Current attention is directed primarily at

pre-saturation dispersal because it is this type that is both quantitatively most important and most strongly subject to natural selection. Four categories of pre-saturation dispersal are suggested (Table 1). These are not mutually exclusive nor likely to be exhaustive. They are based on the circumstances surrounding particular dispersal events.

a. ***Seasonal dispersal*** occurs regularly at particular seasons of the year. It is generally independent of density or other potentially important nonseasonal motivating factors. An example is the commonly reported re-organization of small mammal populations that occurs just prior to and at the beginning of breeding seasons.
b. ***Ontogenetic dispersal*** is that which occurs at a particular developmental stage. In small mammals this typically occurs among juveniles or around the time of sexual maturity.
c. ***Colonizing dispersal*** occurs when individuals move into empty habitat patches and establish homes there. This can occur as a consequence of other types of dispersal whenever a disperser happens to discover suitable open habitat. It can also occur independently of other motivations when a resident individual becomes aware of empty habitat either because it is adjacent to its home range or because it has been discovered on an exploratory excursion.
d. ***Interference dispersal*** is that type which is motivated by the presence of some other species of organism that renders a home range less desirable. Predators, parasites, or competitors are the obvious agents of interference. Fulk (1972) has described how ***Microtus pennsylvanicus*** shifts its activity area and even increases exploratory behavior in the presence of the predatory shrew ***Blarina brevicauda***.

THE NATURE OF DISPERSERS

Considerable effort has been directed toward characterizing dispersers. This is important because, to the extent that dispersers as a class differ from residents, profound ecological and evolutionary consequences may accrue. These efforts have been hampered by: (1) the considerable technical difficulties of identifying dispersers (Lidicker 1985b) and (2) the generally unappreciated heterogeneous nature of the dispersal process. The results so far provide very few generalizations that can be applied to small mammal dispersers. In the future, much better characterization should be possible as technical difficulties are resolved and attention is focused on particular subclasses of dispersal. We should anticipate that different classes of dispersal will be characterized by different kinds of individuals with varying motivations for leaving home. Predicted properties of saturation and pre-saturation dispersers have already been summarized.

It is often the case among small mammals that males are the more dispersive sex (Greenwood 1980, Dobson 1982), although numerous cases are known in which both sexes disperse equally (Lidicker 1975, Greenwood 1983). I am aware, however, of only two cases for which female dominated dispersal is claimed to characterize a

species of small mammal. Meredith (1974) makes such a claim for a small sample (n = 6) of long-distance dispersers in the least chipmunk (***Eutamias minimus***), and Brandt (this volume) reports females dispersing farther than males in some colonies of the pika (***Ochotona princeps***). Dobson (1982) proposes that non-sex-biased dispersal is correlated with monogamy. Typically, the sex ratio varies with the type of dispersal. For example, saturation dispersers in ***Microtus*** are either not sex biased or favor females (Lidicker 1985).

The reproductive state of dispersers also depends strongly on the kind of dispersal involved. Dispersing juveniles are often on the verge of reproductive maturity. Sometimes, at least, this involves the breaking of reproductive inhibition perpetrated pheromonally by like-sexed parents. A particularly well-documented case of this is the prairie vole ***Microtus ochrogaster*** (Getz and Carter 1980). On average this means that dispersing juveniles become reproductively mature at an earlier age than those that remain at home. Saturation dispersal often occurs at times of declining carrying capacity; conditions are severe and reproduction is turned off. In contrast to this, male-biased dispersal at the beginning of the breeding season invariably involves reproductively competent adults. A surprising finding is that in a number of species, pregnant or recently lactating females disperse to new homes leaving their previous home ranges to their last-weaned litter. This has been described for the black-tailed prairie dog ***Cynomys ludovicianus*** (King 1955) and 10 species of microtine rodents (Jannett 1980).

Interest in the behavioral attributes of dispersers has been pursued most actively in the context of attempts to understand the multi-annual cycles of microtine rodents. This is because the Chitty-Krebs model, referred to earlier, requires a genetic polymorphism in the behavior which controls aggression and/or dispersal. A well-supported generalization for these rodents is that dispersers are less aggressive than residents. Whether or not this difference has a genetic basis is a hotly debated issue (reviewed in Lidicker 1985b). My own bias is to view this difference as phenotypic, with residents being characterized by the greater aggressivity associated with territoriality.

The larger issue concerning whether or not dispersers are a genetically distinct subset of a population has been extensively investigated. For a general discussion of the genetic basis of dispersal behavior, see Lidicker and Caldwell (1982, part I). Of particular interest is the question of genetic polymorphisms for dispersal. These are known to be widespread in some groups such as insects (Southwood 1962). For small mammals, two approaches have been utilized extensively. The first is to search for biochemical polymorphisms which may, fortuitously, be correlated with dispersal behavior. A review of the available data (Lidicker 1985b) leads me to the conclusion that while dispersal may be nonrandom in some cases, with respect to particular allozyme genotypes, no consistent associations with dispersal have been found. The second approach has been to plot the frequency distribution of dispersal distances. Assuming that habitat discontinuities are not implicated, a bimodal distribution is then interpreted to imply the existence of both short and long distance morphs. Such distributions have been described for ***Peromyscus maniculatus*** (Howard 1960),

Perognathus formosus (French, Tagami and Hayden 1968), ***Dipodomys merriami, D. microps*** (males only) and ***Perognathus longimembris*** (Allred and Beck 1963). A lack of bimodality, however, has been found in many more instances.

Another possibility is that dispersers may have higher levels of heterozygosity on average than residents. Some support for this is provided by the biochemical data, in that heterozygotes are sometimes found to predominate among dispersers in the genus ***Microtus*** (Lidicker 1985b). More persuasive is the conclusion by Garten (1977) that there is a positive association between exploratory activity and heterozygosity at a series of biochemical loci in ***Peromyscus polionotus***.

Finally, Tamarin (1977) reports that the frequency of a white forehead blaze is higher among dispersers of ***Microtus breweri***, and Lidicker (1976) found a higher frequency of albino pelages among feral house mice (***Mus musculus***) attempting to escape from two large experimental enclosures.

FUTURE DIRECTIONS

I expect that small mammals will continue to provide interesting and productive subjects for studies of dispersal. Extensions into new directions such as navigation will surely be important (Mather and Baker 1980, 1981; Hoeck 1982). Much more needs to be learned regarding the genetic basis of dispersal and its behavioral and physiological underpinnings. When further explored, the extent and nature of true migratory movements (back and forth) among small mammals may produce surprising results. Certainly a variety of spatial arrangements, social dynamics, and demographic patterns are available against which various evolutionary and demographic questions can be pursued. This should include the possible role of interdemic selection in the evolution of dispersal.

Predicated on the acceptance of the heterogeneous nature of dispersal, a whole new generation of investigations needs to be pursued in which the kinds of dispersal can be clarified. As with other areas in biology, diversity should be acknowledged and appreciated, not forced into conformity with unrealistic simplifications and generalizations. Concordant with this is the need to define the nature of dispersers and their motivations for moving, in numerous particular instances. Only then can a comprehensive understanding of this critically important class of phenomena be developed.

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THE EVOLUTION OF SEXUAL DIFFERENCES IN NATAL DISPERSAL: A TEST OF GREENWOOD'S HYPOTHESIS

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ABSTRACT

Recently, P.J. Greenwood proposed that sexual differences in natal dispersal were by-products of mating systems. Specifically, if males defend resources in order to attract mates, females rather than males will be selected to disperse. Greenwood suggested that males will be hampered in their attempts to acquire breeding space away from their places of birth by the territorial activities of adult males, but because females do not defend territories, females will be free to disperse to areas with better resources or fewer male relatives. If males defend mates instead of resources, then male dispersal will be favored.

To test this hypothesis, the breeding and dispersal patterns of a population of pika (*Ochotona princeps*) were studied over a three-year period. These animals were found to exhibit predominantly female natal dispersal. The single most important factor influencing female reproductive success was whether or not females denned in holes or in open talus. Suitable denning holes were found to be in short supply and distributed such that males could defend them. Males defending such holes mated more consistently and sired more offspring than did other males. Males did not herd or attempt to influence the movements of females; thus the suggestion that resource defense mating systems and female natal dispersal are linked was upheld. The causal connection that Greenwood proposed to link the two phenomena was not supported, however, as both sexes of pika were found to defend similarly-sized territories during the dispersal period of juveniles.

INTRODUCTION

The dispersal of individuals from one locale to another is a fundamental ecological process. Natal dispersal may be defined as the movement an animal makes from its place of birth to another area where it reproduces or attempts to reproduce (Howard 1960). Within populations, variation in dispersal tendency or natal site tenacity is common: particular subsets of populations show consistently lower site tenacity than others. This paper focuses on one aspect of this variation, namely, the tendency for one sex to perform the major share of dispersal in a population.

The taxonomic distribution of sexual differences in natal dispersal is striking. Among mammals, the predominant dispersal of females is rare, being known in only five species (Greenwood 1980). In contrast, the predominant dispersal of males is rare among birds (Greenwood op. cit.). This nonrandom distribution of dispersal patterns suggests the operation of a single, fundamental cause for sexual differences in dispersal.

One commonly accepted hypothesis concerning the evolution of sexual dispersal patterns was proposed by P.J. Greenwood (1980). He suggested that the manner in which males gain access to mates will determine whether males or females are the predominant dispersers. Generally, males may defend resources, such as nesting sites and food sources, as a means of acquiring mates (Verner 1964), or they may directly sequester females without defending resources (Bradbury and Vehrencamp 1977). Greenwood suggested that male natal dispersal would be favored if males defend females rather than resources, because males would be able to gain more, reproductively, from local variation in sex ratios than could females. Thus young males would emigrate from areas or groups containing fewer females per male to areas with more favorable sex ratios. If males defend resources, females should be the predominant dispersers. Greenwood reasoned that young males, because of the territorial activities of other males, would be hampered in their attempts to acquire breeding space away from their places of birth. Familiarity with the natal area would, in contrast, make that area more valuable than an unfamiliar one. Also, familiarity could be an important factor in determining the outcome of competition for breeding sites. Females, because they are not territorial, would be free to disperse from their natal areas and could thereby enhance their reproductive output by avoiding close inbreeding and gaining access to areas with more or better resources.

This paper concerns a test of this hypothesis. Pika (***Ochotona princeps***: Lagomorpha) have been suggested to exhibit predominantly female dispersal (Millar 1971). If this trend in dispersal is confirmed, the predictions from Greenwood's hypothesis are: (1) male pika should defend resources rather than mates, and (2) males, not females, should defend territories during the period when juveniles disperse.

METHODS

Pika are small (150 g adult weight), diurnally active, montane mammals of western North America. They are almost strictly confined to talus areas where they occupy the talus-meadow ecotone. Both sexes breed as yearlings, producing 2 to 3 young in each of 2 consecutive litters (Millar 1973). Pika do not hibernate in the winter; instead they feed on vegetation which is gathered during the summer and stored in haypiles. By the start of the haying period, all young are weaned and have begun to disperse and establish themselves in the population. Pika are quite vocal, giving 3 distinct types of vocalizations: a short call, a long call and a submissive squeak. The short call is believed to be associated with territory maintenance (Svendsen 1979).

I studied a population of pika which occupies 5 ha of limestone talus in northeastern Oregon (44°48'N, 118°5'W) at 1900 m elevation. The entire study area was divided into 5- by 5-m squares with numbered stakes as reference points. Studies were conducted from 10 May to 1 September of 1980 through 1982. All animals on the site were live-trapped, weighed, sexed and given numbered and color coded ear tags before being released at the point of capture. No significant departures from 1:1 sex ratios were found.

All individuals in the population were observed in a random sequence for 15 minutes per animal per observation period. Continuous notes of the focal animal's location and activities were made. A digital watch was used to make temporal references to the start and termination of each activity. From these data, activity fields (Waser and Wiley 1979) were computed that consisted of all 5- by 5-m quadrats visited by an animal during a given period of time. The "diameter" for each activity field was calculated from a circular range of the same area as the activity field. Encounters between animals were defined to be instances when animals were less than 2 m apart.

The reproductive period extended from early May to early June. Mated pairs were determined from direct observations of copulations and extrapolation of associated behavior, such as male sentinel activity outside the den of a female with young. Juveniles were live-trapped, marked and sexed as they appeared outside their dens. Litters were ascribed to the adult pair associated with the den. No adult female was seen within 10 m of another's den, so little error was associated with this method. By 1 September, most first-litter juveniles were established in or very close to areas where they could be found the following spring, if they could be found on the study site at all. The closest suitable talus was over 4.5 km distant, and no tagged animals were ever found there. Thus disappearances from the study site were presumed to be equivalent to death. Dispersal distances were calculated as the straight line between the center of each juvenile's activity field during August and the animal's natal den.

Several characteristics of the dens and their surroundings were measured. The shortest distance from the den to vegetation (DISVEG) was measured. The percent cover of grasses (GRASS) and dicot herbaceous vegetation (HERB) near the den was determined from randomly scattered ¼- by ¼-m squares. Talus dimensions (ROCK) near dens were estimated from diameter measurements (in ¼-m increments) of rocks at 9 grid points of a 3- by 3-m grid centered on each den. Finally, dens were classed according to whether they were in a naturally formed hole or were in the open talus (NEST). These data along with measurements of maternal and paternal ages (MAGE, PAGE) and body weights (MBW, PBW) were subjected to a multiple regression analysis to discover which factors had the greatest influence on the number of offspring weaned per female per year (hereafter "female reproductive success").

The locations of all holes that might have been used as dens were plotted on scale maps of the study site. Lloyd's Index of Patchiness (Lloyd 1967) was calculated using quadrats the size of the average activity field of males as determined during the haying period. Index values greater than 1 indicate a distribution clumped on the scale of the quadrat used in the calculations and thus a resource that could be defended

by individual male pika.

Mean values are reported plus-or-minus one standard error. Data were transformed, when necessary, to conform to normality assumptions.

RESULTS

By their first September, juvenile female pika were found farther from their natal dens than were juvenile males (Fig 1A). Males also bred closer to their places of birth than did females (Fig 1B). No significant sexual differences were found in the sizes of adult activity fields during the haying period (males: 923 ± 78 m^2 (15); females: 944 ± 81 m^2 (14); $t = 0.18$), thus the metric distances of dispersal were not influenced by sexual differences in adult dispersion.

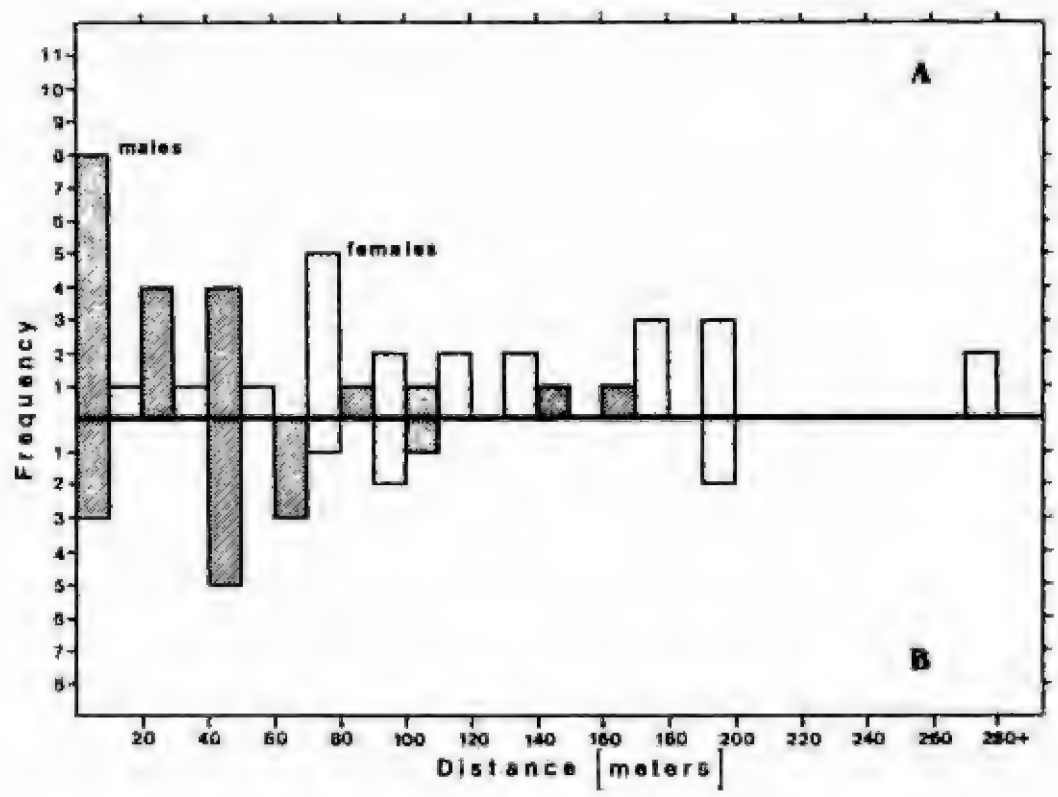

Figure 1

Distances moved by first-litter juvenile male and female pika from their places of birth to (A) their August residences (1980–1982) and (B) their first breeding sites (1981–1982). Kolmogorov-Smirnov two-sample test: (A) $p < 0.0002$; (B) $p = 0.033$.

The conditions for the evolution of resource defense mating systems (Borgia 1979, Bradbury and Vehrencamp 1977) are: (1) some resource other than males must limit female reproductive success; (2) this resource must be economically defendable; and (3) male reproductive success must be correlated with the resources he defends. Evidence that can be used to infer that males defend resources rather than mates is: (1) male territorial activities are tied to resource quality and not to the presence or absence of females nearby (Cronin and Sherman 1977), and (2) males do not herd or interfere with the movements of females (Bradbury 1980).

Table 1

Hierarchal multiple regression analysis of the effects of year, maternal, paternal and habitat factors on the number of offspring weaned by female pika.

Variable Set	Increment R^2	d.f.	F	*p*
Year	0.0314	1,28	0.910	0.35
Maternal	0.0690	2,26	0.997	0.32
Paternal	0.0437	3,23	0.390	0.75
Habitat	0.6324	5,18	10.051	< 0.001

FRS = 0.08	− 0.29 YEAR	+ 0.12 MAGE	+ 0.03 MBW	− 0.37 PAGE
(*t*-test)	(−1.75)	(0.61)	(0.16)	(−1.96)
+ 0.64 PBW	− 0.24 PAGEPBW	+ 1.40 NEST	− 0.08 GRASS	+ 0.26 HERB
3.29**	(−1.30)	(5.19***)	(−0.58)	(1.93)
− 0.07 DISVEG	+ 0.38 ROCK			
(−0.46)	(1.81)			

** $p < 0.01$

*** $p < 0.0001$

See text for abbreviations.

The results of the multiple regression analysis indicate that resources other than males limited the reproductive success of female pika (Table 1). Characteristics of the den area accounted for more than 60% of the variation in female reproductive success, with the most influential variable being whether or not the den was made in a hole or the open talus. All else being equal, females denning in holes weaned 1.4 more young than females that denned in open talus (over all, females weaned 2.6 ± 0.3 offspring/year/female). The number of offspring weaned per female was strongly correlated with the number of young surviving to adulthood ($r = 0.78$ (18), $p < 0.0001$), but was not significantly related to maternal survival ($r = 0.28$ (20), $p > 0.5$).

The second condition for the evolution of a resource defense mating system, namely that resources be defendable, was also met. Potential denning holes were not distributed at random but were strongly clumped (Lloyd's Index: 4.99 ± 0.60, $n = 4$ quadrats of study site). Furthermore, areas with suitable den holes were scarce relative to the number of females in the population (Table 2). Fifteen areas the size of the average activity field of the adult females contained potential den holes. These areas were almost always occupied by females every year (% occupancy: 98% ± 2%, $n = 2$ years); females that failed to den in holes had no holes in their activity fields, nor were any nearby.

Table 2

Number of sites with suitable den holes per female on study site at three times of the year.

Date	No. Sites per Female ± s.e.[a]
May 10[b]	0.910 ± 0.028
June 10[c]	0.417 ± 0.019

[a] n = 2 years (1981–1982).

[b] Corresponds to start of reproductive period.

[c] Corresponds to beginning of dispersal period.

[d] Corresponds to end of haying period.

Finally, the reproductive success of male pika was correlated with the quality of resources they defended. Males whose activity fields encompassed potential den holes were more likely to have had a female living close by than were males without suitable den holes (Table 3A), and as a result, males holding suitable dens were more likely to have mated (Table 3B). Such males sired more weanlings per year (2.9 ± 0.4 (28)) than did males without suitable den holes (0.6 ± 0.4 (8), $t = 3.204$, $p < 0.003$). This difference was not due to variation in male age or size, as these factors of themselves had insignificant effects on female reproductive success (Table 1).

Several observations indicate that male pika defended resources rather than females. Males defended territories during the mating period: all males excluded others from a portion of their activity fields. When the resident male was experimentally removed ($n = 7$), his formerly exclusive area was invaded within 24 hours. Male territorial activities were not significantly influenced by whether or not a male had a mate (Table 4). Unmated males gave short calls as frequently as mated males, held similar portions of their activity fields in exclusion of other males and were as aggressive toward intruding males as were mated males. The contrast between males with and without suitable den holes was marked (Table 5). The activity fields of males without den holes were less exclusive of neighboring males, and males without den holes called less often. Encounters between animals were too rare to allow comparisons on this basis.

No herding of females was ever observed. During the mating period, encounters between sexes (40) were more frequent than encounters between animals of the same sex (22), yet intersexual encounters comprised only a small fraction of the time the males were under observation (9.0% ± 2.5% (10 males)). Intersexual encounters were usually passive (35 of 40), involving no chases or spatial displacements of either animal. All instances of aggression involved females chasing males. Furthermore, a good deal of each female's activity field was outside the activity field of her mate during the mating period (58% ± 5% (15 females)), thus much of the activities of females were outside the influence of their mates.

Table 3
Effect of defense of suitable den holes on the reproductive success of male pika.

	Suitable den hole in male's activity field?	
A.	Yes	No
Number of cases of female activity center ≤ D + S[a] from male activity center	27	3
Number of cases of female activity center > D + S[a] from male activity center	1	5
	(Fisher's exact $p = 0.0008$)	
B.		
Number of cases male mated	25	4
Number of cases male unmated	3	4
	(Fisher's exact $p = 0.03$)	

[a] D = mean diameter of activity fields during haying period.
S = standard deviation of above distribution

As noted earlier, adult females occupied activity fields during the haying period which were no smaller than the activity fields of adult males. Both sexes exhibited territorial behavior during the haying period, with no significant sexual differences on the basis of any measure of territoriality (Table 6). Females emitted advertisement calls as often as did males; they were as aggressive toward other adults, and they excluded other adults from similar portions of their activity fields. In all cases, each ***female's*** exclusive area was rapidly invaded by other adults once the resident was removed.

DISCUSSION

Greenwood's hypothesis is in part a statement that a population's mating system will cause that population to evolve a particular dispersal pattern. In this regard, one prediction of this theory is that a particular mating system, e.g., one in which males defend resources rather than mates, and a particular natal dispersal pattern, e.g., the predominant dispersal of females, will be found in the same population. This prediction was upheld for pika: pika exhibit both a resource defense mating system and the predominant dispersal of females. The conditions thought to be necessary for the evolution of a resource defense mating system (Borgia 1979, Bradbury and Vehrencamp 1977) were shown to have been present, and pika's social behavior

Table 4

Evidence for territoriality of male pika during reproductive period: contrast by mating status

	Mated Males	Unmated males	*p*
Percent activity field exclusive of other males	82.3 ± 5.2% (15)	88.4 ± 4.4% (6)	> 0.5 [a]
Number of short calls given per 10 minute interval	2.1 ± 0.4 (6)	1.6 ± 0.3 (6)	> 0.5[a]
Number of aggressive encounters with intruders out of total number of encounters	10/12	5/5	0.49[b]

[a] *t*-test
[b] Fisher's exact

Table 5

Evidence for territoriality of male pika during the reproductive period: contrast by quality of resource defended.

	Males with suitable den holes	Males without den holes	*p*
Percent activity field exclusive of other males	90.3 ± 9.6% (13)	75.0 ± 6.7% (4)	< 0.03[a]
Number of short calls given per 10 minute interval	2.4 ± 0.3 (13)	1.2 ± 0.3 (4)	< 0.05[b]

[a] Mann-Whitney U = 5.5
[b] $t = 2.338$

conformed to that predicted for animals that defend resources rather than mates. That females were the predominant dispersers was clear from the observation that female pika were found farther from their places of birth than were juvenile males both at the end of their first haying period and at the beginning of their first mating period.

Mating systems based upon the defense of resources are rare among mammals, perhaps occurring in no more than 15% of species (Brandt 1984). Five mammalian species are known to exhibit female natal dispersal. The mating systems of only two of these five species have now been studied, and in both cases (pika and the white-lined bat *Saccopteryx bilineata*, Bradbury and Vehrencamp 1977) a resource defense mating system was found. By chance, such a result would be expected only 2.5 times out of a hundred.

Table 6
Evidence for territoriality of adult male and female pika during the haying period.

	Males	Females	*p*
Percent activity field exclusive of other adults	49 ± 4% (17)	48 ± 5% (13)	> 0.5[a]
Number short calls given per 10 min interval	2.0 ± 0.2 (17)	1.8 ± 0.2 (13)	> 0.3[a]
Number of aggressive encounters with intruder adults out of total number of encounters	7/10	13/22	> 0.5[b]
Number of cases exclusive area invaded within 24 hrs. after removal out of total number of removals	7/7	5/5	1.0[c]

[a] *t*-test

[b] χ-square test

[c] Fisher's exact

Greenwood's hypothesis is also a logical statement outlining the presumed causal connection between resource-defense mating systems and female natal dispersal. In resource-defense mating systems, the reproductive success of both sexes depends upon the relative quality and quantity of resources to which they have access. All animals, regardless of sex, that find themselves in areas with poor quality resources could theoretically make reproductive gains via dispersal to better areas. Consequently, no sexual differences in dispersal would be expected unless other factors constrain the movements of males or otherwise make the movements of females more likely. The mechanism that Greenwood suggested would hinder male dispersal was sex-dependent territoriality. He noted that where resources are to be found in the same locales from one breeding period to another, animals may make use of the competitive advantages that accrue from site familiarity in settling their territorial disputes. Territorial males competing for space away from their natal areas would thus be at a disadvantage relative to residents. Because they do not defend territories, emigrant females would not be at such a disadvantage and would be free to disperse.

The present study has shown sex-dependent territoriality to be an unnecessary condition for the predominant dispersal of females. Sex-dependent territoriality may be a sufficient condition for the predominant dispersal of females in species with resource-based mating systems, but other mechanisms are apparently as effective. One such mechanism may be inbreeding depression, which usually results when

closely related individuals mate (e.g., Haigh 1983; Ralls, Brugger and Ballou 1979). Inbreeding will generally be more costly for females than for males in polygynous populations (Clutton-Brock and Harvey 1976, Smith 1979). Thus more females than males might be able to benefit from dispersal even though dispersal is constrained by the territorial activities of others. Females of species using resource rather than mate defense tactics would be expected to disperse (a) if ample improvement in resources could be had by doing so, or (b) if they could not outbreed in their natal areas. Where inbreeding costs are low or where females have outbreeding opportunities on their natal areas, female natal dispersal may be no more likely than male natal dispersal. Where inbreeding costs are heavy and females are unable to outbreed on their natal areas, female dispersal should predominate.

Pika seem to fit the latter condition. Observed instances of father-daughter and mother-son matings produced approximately 60% fewer weaned young than did matings between less-related individuals (Brandt, unpublished data). Fourteen percent of males mated with more than one female in a year, and males lived longer than females (Brandt 1984). Thus inbreeding costs would be heavier, on average, for females than for males. Furthermore, because the same males held tenure in the same breeding sites for several years (Brandt 1984), few females would have been able to avoid incest without emigrating from their places of birth.

Sex-dependent territoriality and inbreeding costs may be equally potent forces favoring female rather than male natal dispersal among many species that exhibit resource-defense mating systems. Whether or not such a plurality exists could be tested by examining truly monogamous species where males defend resources and females do not. Future theories and exploration of the causes of natal dispersal patterns must also incorporate mating systems other than resource or mate defense, such as lek systems. Finally, as this study suggests, no single line of causation may lie behind all dispersal patterns. Comprehensive hypotheses may need to be pluralistic rather than simplistic.

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ENDOCRINE INFLUENCES ON NATAL DISPERSAL IN BELDING'S GROUND SQUIRRELS *(SPERMOPHILUS BELDINGI)*

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ABSTRACT

The purpose of this study was to attempt preliminary identification of the physiological causes of natal dispersal in two populations of Belding's ground squirrels (***Spermophilus beldingi***) living at different elevations in the Sierra Nevada of California. We tested two competing hypotheses, each suggesting a different endocrinological cause for natal dispersal in this species. Data collected by observation, trapping and telemetry during three field seasons (1979–1981) contradict predictions of the hypothesis that concurrent, high levels of circulating gonadal steroids cause natal dispersal. Rather, the data tentatively suggest that perinatal exposure to androgen subsequently results in dispersal of treated individuals. The hormone may engender dispersal behavior through its mediating effects on juveniles' exploratory and social behaviors. Possible interactions of endocrine mechanisms with other proximal and ultimate causes of dispersal are discussed.

INTRODUCTION

Sherman (1977) and Holekamp (1984) observed a marked sexual dimorphism in natal dispersal in Belding's ground squirrels (***Spermophilus beldingi***): young males emigrated from their natal areas, but females were usually philopatric. This sex difference in dispersal behavior is typical of that found in most mammals (Dobson 1982, Greenwood 1980). The purpose of this study was to attempt preliminary identification of the physiological mechanisms of dispersal behavior in this species. We hypothesized that dispersal might be mediated by endocrine activity, in particular

by gonadal steroid hormones. Earlier work with both insect dispersal (Caldwell 1974, Caldwell and Rankin 1972, Johnson 1969) and migration in fish, amphibians and birds (Meier and Fivizzani 1980) indicated that hormones function importantly in the regulation of long-distance movements in these organisms. Androgens were most strongly suggested as control agents for natal dispersal in *S. beldingi* because males emigrate but females remain in their natal areas.

Much recent work in behavioral endocrinology has focused on the ontogeny and hormonal mediation of sexually dimorphic behavior patterns in mammals. From this body of research has emerged the finding that gonadal steroids can affect adult behavior in two general ways: (1) by acting during fetal and/or neonatal life on neural tissues later destined to mediate dimorphic behavior patterns (Arnold 1980, Toran-Allerand 1978, Whalen 1982), and (2) by direct action on neural and other substrates in the adult organism (McEwen 1981). Phoenix, Goy, Gerall and Young (1959) chose the terms "organizational" and "activational," respectively, to describe these two modes of hormone action.

An activational hypothesis suggests that natal dispersal is caused by high levels of circulating androgen at the time of dispersal. It therefore predicts that blood titers of androgen should be elevated during the dispersal period. This hypothesis also predicts that castration of pre-dispersal males, by eliminating the source of androgen, should feminize dispersal behavior. Thus castrated males should fail to disperse, whereas females treated with exogenous androgen and sham-operated males should exhibit masculine dispersal behavior. Similarly, if philopatric behavior in females is facilitated by ovarian hormones, then ovariectomized females should exhibit masculinized dispersal behavior. By contrast, an organizational hypothesis suggests that the physiological cause of natal dispersal is exposure of the pre- or early post-natal nervous system to androgens. The organizational hypothesis predicts that treatment of perinatal females with androgen should masculinize their dispersal behavior.

METHODS

Spermophilus beldingi is a group-living, diurnal rodent inhabiting alpine and sub-alpine meadows in the Sierra Nevada of California. With nine student assistants, we monitored the dispersal behavior of these animals during the periods from 20 April to 17 September 1979, 16 April to 16 September 1980, and 13 April to 9 September 1981. During the three-year study period we observed these animals for 2337 hours and permanently marked 1698 animals with ear tags and toe clips as described previously (Holekamp 1983). We also marked all animals in observation areas with individually distinct patterns of hair dye.

Our two study sites in Mono County, California, comprised a 3.13 ha meadow in lower Lee Vining Canyon (henceforth LVC; 38°56′N, 119°10′E, elevation 2246 m), and a 4.14 ha meadow 13 km west in the Harvey Monroe Hall Natural Area (henceforth HMH; 38°57′30″N, 119°17′E; elevation 3050 m).

We adopt Lidicker's (1975) definition of dispersal. Thus natal dispersal involves complete and permanent departure from the natal area prior to attainment of reproductive maturity. An individual's natal area was the home range of its mother when it first emerged from the natal burrow. Because the largest home range of any dam at that time had a radius of 80 m, "natal area" was operationally defined as the area of a circle 160 m in diameter with the natal burrow at its center. An individual was classified as a disperser if, after its activity ceased in the natal area, it was eventually relocated by means of observation, trapping, telemetry, or identification as a road kill (Holekamp 1984). Activity in the natal area was considered to have ceased when the individual was not trapped, telemetered, or seen there during daylight hours and also failed to spend the night there.

All juveniles were trapped and marked at their first emergence from their natal burrows, approximately 27 days after birth. Marked squirrels were observed daily, as described elsewhere (Holekamp 1983). To discriminate between true dispersal and mere exploratory excursions and to delimit the age range during which dispersal occurred, we conducted "nightwatch" each evening in both study meadows. That is, observers were present in the meadows at sunset to determine whether juveniles were still spending the night in their natal areas. Beginning 18 days after a litter's first emergence above ground, each observer watched a single litter each evening and noted burrows entered by litter members.

Between 60 and 97 days after their births we attempted to recover individuals born in our meadows using 4 techniques (Holekamp 1984). (1) We conducted extensive visual searches for dispersers in habitat peripheral to HMH, up to 4 km from its center. (2) Where visual scanning was impossible due to vegetation height (LVC), we set baited Tomahawk traps at 20 m intervals in large grids, up to 4 km from the center of the meadow. (3) We collared 51 juveniles (40 males, 11 females) with radio transmitters before they dispersed and tracked them on alternate days. (4) We examined all road-killed rodents in Lee Vining Canyon. When a marked squirrel was relocated by any of these methods, its distance from its natal burrow was later established with large-scale aerial photographs.

To test the activational hypothesis we bilaterally gonadectomized 59 males and 19 females and performed sham surgeries on 19 males and 6 females. The mean age at which surgeries were performed was 33 ($\pm$ 11) days for males and 39 ($\pm$ 6) days for females. All surgeries were performed in the field. Operated animals were held in traps until they recovered from anesthetic (Metofane) effects and then were returned to their natal burrows after a mean period of 3.6 h. To monitor plasma androgen levels in young males, 6 litters were born and reared in captivity and blood samples were drawn from their 26 male members at 3-wk intervals throughout the juvenile summer. Animals were anesthetized with Metofane, and 1.25 ml plasma was removed via capillary tubes inserted in the ocular orbit (Riley 1960). Successive bleedings alternated between left and right eyes. Plasma was stored at $-70°C$ until assayed. Testosterone content in blood samples was determined by radioimmunoassay (RIA) as described by Licht, Zucker, Hubbard and Boshes (1982). The minimum detectable level of testosterone in the RIA analysis was 0.05 $ng \cdot ml^{-1}$.

To test the organizational hypothesis we maintained eleven pregnant *S. beldingi* in captivity until their litters were born. Within 36 hours of birth, all female offspring from 9 litters were injected subcutaneously with 500 μg of testosterone propionate (TP) in 0.05 ml sesame oil. All female offspring from 2 control litters were treated with 0.05 ml oil alone. At dawn on the day following this treatment, each dam and her offspring were transported together to HMH and released there.

RESULTS

Activational Effects

Untreated males and females from marked cohorts first showed sex specific differences in mean minimum distances of recapture point from their natal burrows during the third month after birth, and these differences persisted and increased with age (Fig 1). Table 1 compares recovery of untreated squirrels with recovery of operated subjects. Of 158 untreated females recovered after 60 days of age, only 12 (8%) had dispersed, whereas 68 of 92 recovered males (74%) had emigrated. Thus males were significantly more likely to disperse than were females ($\chi^2 = 117.52$; df = 1; $p < 0.001$). Neither castrated nor sham-operated animals differed significantly from untreated individuals of the same sex.

Dispersal occurred most commonly when untreated males were 9–10 weeks of age. Although castration did not significantly reduce the probability of male dispersal (Table 1), operated males dispersed significantly more frequently during later age intervals than did untreated males (Fig 2: $\chi^2 = 28.051$; df = 5; $p < 0.001$). Sham-operated males ($n = 6$) also tended to disperse during later age-intervals than did untreated males. Thus surgical trauma apparently retarded dispersal, but removal of the testes did not significantly change the probability that males would disperse. Radioimmunoassay results showed that androgen levels in male *S. beldingi* were consistently very low (< 0.3 ng·ml^{-1}) throughout the juvenile summer, and there was no elevation of these levels during the primary dispersal period (Holekamp, Smale, Simpson and Holekamp 1984).

Organizational Effects

Transplanted litters contained 21 TP-treated females, 6 oil-treated females, and 17 males. Twelve hormone-treated females were recovered when they were at least 60 days old (Table 2); none of the oil-treated females were recovered. Table 2 suggests that neonatal TP-treatment engendered masculine dispersal behavior in experimental females. Chi-square comparisons of numbers of dispersers in each group revealed that TP-treated females differed significantly from untreated females, but not from males. Transplanted males did not differ significantly from resident males in their tendency to disperse.

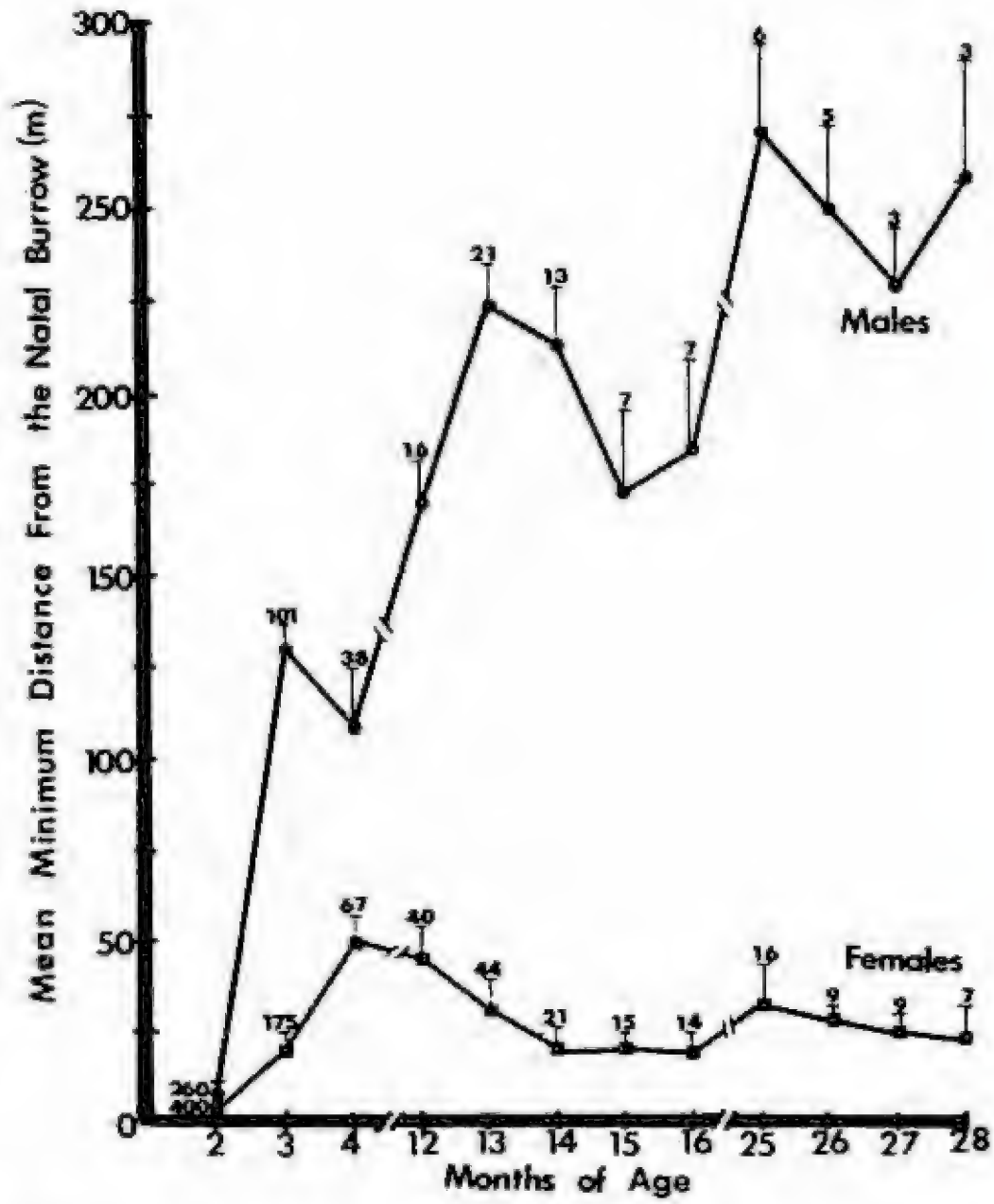

Figure 1

Mean minimum distances from the natal burrow at which marked male and female *S. beldingi* were relocated during their first three years of life. Vertical bars represent standard errors and numbers represent sample sizes. Data from HMH and LVC animals have been aggregated.

Analysis of variance of mean minimum distances from their natal burrows at which TP-treated females, their brothers, and untreated juveniles were found during their first summers revealed no significant differences between the male groups nor between either male group and TP-treated females (Fig 3). All three of these groups, however, differed significantly from untreated females.

Finally, frequencies of several exploratory, locomotor, sexual and play behaviors were found to differ significantly between TP-treated and untreated females but not between transplanted and resident males (Holekamp et al. 1984).

Table 1
Chi-square comparisons of normal and operated male and female *S. Beldingi* with respect to dispersal.

Groups Compared	Number Dispersed	Number not Dispersed	χ^2	p
Unoperated Males	68	24		
Unoperated Females	12	146	117.520	$< 0.001^*$
Unoperated Males	68	24		
Gonad-X Males	19	2	2.644	> 0.10
Unoperated Males	68	24		
Sham-Op Males	6	6	2.958	> 0.05
Unoperated Females	12	146		
Gonad-X Females	1	6	0.914	> 0.10
Unoperated Males	68	24		
Gonad-X Females	1	6	10.951	$< 0.001^*$

* indicates statistical significance ($p < 0.05$)

DISCUSSION

Our test of the activational hypothesis was based in part on hormonal data from captive males. Because we cannot currently evaluate some of the assumptions underlying the use of these data, conclusive interpretation of our results is not yet possible. For example, plasma androgen levels may differ between wild and captive juveniles. Furthermore, blood may have been drawn from captive juveniles too infrequently to detect transient increases in hormone levels. Finally, we cannot rule out the possibility that extragonadal androgens may have influenced dispersal behavior in free-living castrates. However, because circulating testosterone levels were extremely low at the time of dispersal, and castration appeared not to affect dispersal behavior except to retard its occurrence, we tentatively reject the activational hypothesis.

Although this study should be replicated with larger samples and neonatal castration of males, our results offer preliminary support for the hypothesis that perinatal TP exposure did promote natal dispersal in *S. beldingi*. The proportion of TP-treated females that dispersed was significantly larger than that for untreated females but not than that for males. Nor was the mean distance dispersed by TP-treated females significantly shorter than that for males (Holekamp et al. 1984). Their mean dispersal distance was, however, much greater than that for untreated females.

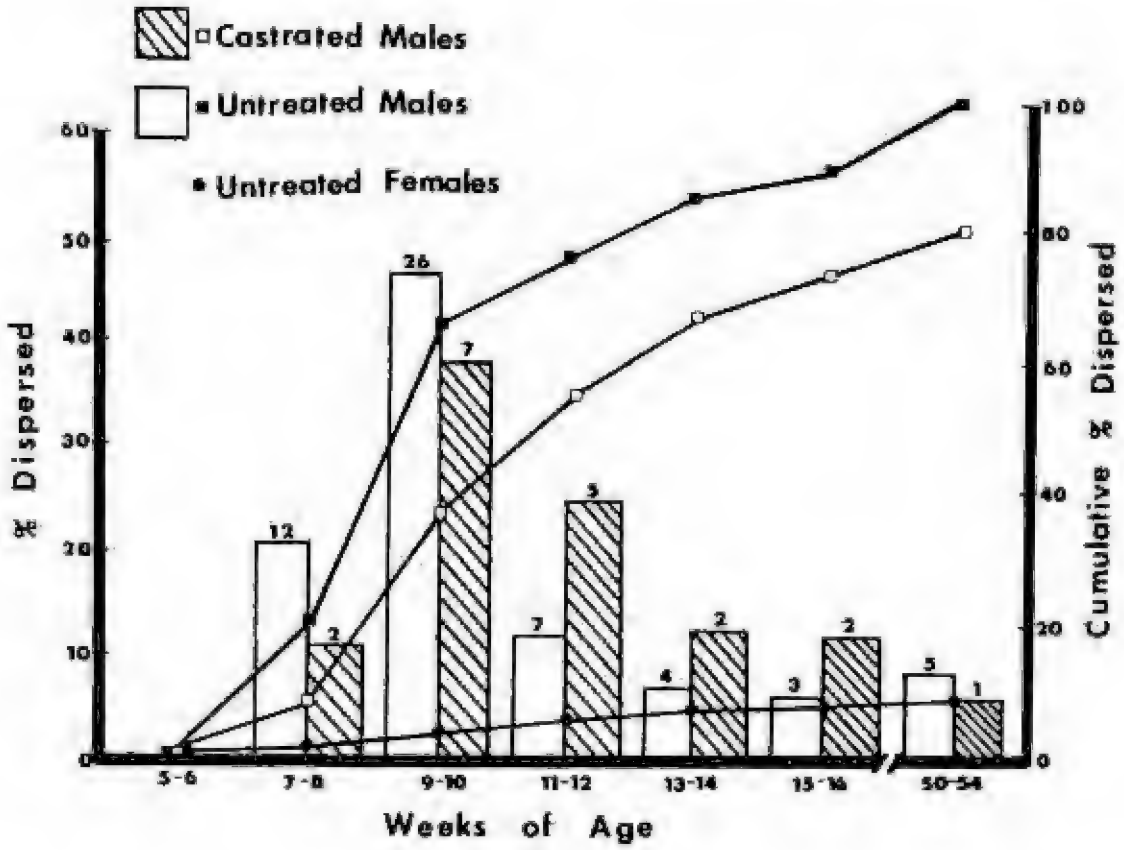

Figure 2

Ages at which dispersal was observed to occur in castrated males and unoperated juveniles whose ages of dispersal were known (by means of telemetry and nightwatch data) to within 10 days. The linear curves represent cumulative percentages of surviving castrates, unoperated males, and unoperated females known to have dispersed during each age interval. Thus, by the end of their 54th week of life, all surviving untreated males and 80% of all surviving castrated males had dispersed.

Because none of the oil-treated control females were observed after their 60th day of age, the hypothesis cannot be ruled out that changes in the dispersal behavior of TP-treated females were induced by transplantation into the meadow rather than by the hormone treatment. However two lines of evidence suggest that TP-treatment induced these changes. First, a partial control for the effects of transplantation was achieved with the male littermates of TP-treated females. Most monitored behaviors of transplanted males did not differ from those of resident males (Holekamp et al. 1984). This indicates that transplantation did not significantly affect juvenile behavior. Second, in addition to dispersal, TP-treatment appeared to masculinize various exploratory, locomotor and social behaviors that are sexually dimorphic in untreated juveniles (Holekamp et al. 1984). These data suggest that TP-treatment selectively affected some monitored behaviors but not others.

The hypothesis that TP-treatment, not transplantation, modified dispersal behavior is also supported indirectly by findings of laboratory workers in behavioral endocrinology showing that exploration, locomotor activity, aggression, play and sexual behaviors are all importantly influenced in other rodents by perinatal androgen secretion (Beatty 1979, MacLusky and Naftolin 1981). Thus, although not conclusive, our results suggest that neonatal TP-treatment masculinized dispersal behavior in experimental females. Perhaps natal dispersal in *S. **beldingi*** is caused physiologically by early androgen exposure of neural substrates underlying exploratory and/or social behaviors. Ontogenetic changes in these behaviors might promote the

Table 2
Chi-square comparisons of TP-treated females and their brothers (transplanted males) with untreated resident juveniles.

Groups Compared	Number Dispersed	Number not Dispersed	χ^2	p
TP-treated Females	8	4		
Normal Females	12	146	37.485	$< 0.001^*$
TP-treated Females	8	4		
Normal Males	68	24	0.283	> 0.10
Transplanted Males	3	2		
Normal Males	68	24	0.468	> 0.10

* indicates statistical significance ($p < 0.05$).

expansion and shift of home range that ultimately results in dispersal from the natal site.

Investigators have long been aware of the ubiquity of dispersal behavior in birds and mammals (e.g.. Farner 1945; Howard 1949, 1960). Yet, even with modern analytical tools, identification of the proximal causes of dispersal has proven quite difficult (Gaines and McCleneghan 1980). Although complete understanding of natal dispersal's physiological mechanisms is far in the future, we have attempted here to develop some methodological and theoretical alternatives to traditional dispersal research that we hope other investigators will pursue.

If the organizational hypothesis is eventually confirmed, it will be consistent with many pertinent data describing not only sexually dimorphic mammalian dispersal patterns but also genetic and endocrine substrates underlying other sex differences and sex differentiation in birds and mammals. That is, in mammals, males are heterogametic (XY), while in birds the reverse is true. The relationship between chromosomal sex, sex differentiation, and subsequent behavioral capacity in birds and mammals has been reviewed by Adkins-Regan (1981), MacLusky and Naftolin (1981) and by Wilson, George and Griffin (1981). Sometime after their formation in male mammals, the testes secrete androgens for a brief period during fetal development. Castration of the male fetus prior to this secretory period results in a morphologically and behaviorally female phenotype. Perinatal exposure of female mammals to androgens results in masculinization (and defeminization) of behaviors that are normally sexually dimorphic. By contrast, perinatal treatment of male mammals with female gonadal hormones (estrogens and progestins) has no analogous effect on dimorphic behavior patterns. Thus sex-typical adult behavior of homogametic mammals can be reversed by prenatal exposure to the gonadal hormone which is normally secreted at this stage of development only in members of the heterogametic sex. This is also true in birds: the developing gonads of the heterogametic avian sex

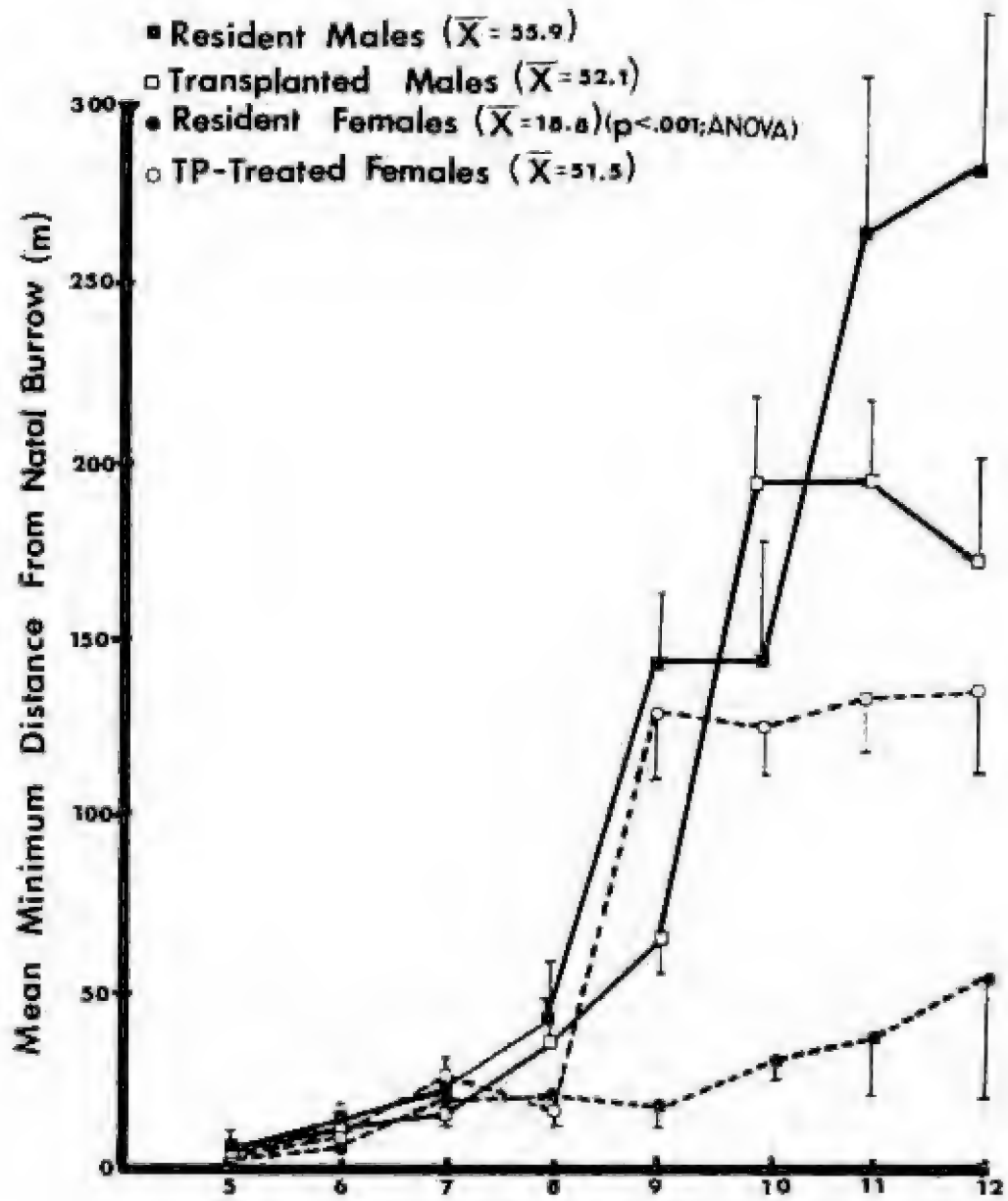

Figure 3

Mean minimum distances from their natal burrows at which TP-treated females, their brothers (transplanted males) and resident juveniles were relocated during their first summer. Initial emergence from the natal burrow (and weaning) occur during week 4. Entry into hibernation begins during week 12. All data are from HMH. Vertical bars represent standard errors. Sample sizes representing numbers of animals are as follows: resident males (n = 93), transplanted males (n = 5), TP-treated females (n = 12) and resident females (n = 158).

(female) normally secrete steroid hormones (estrogens) during a brief embryonic period, and this subsequently results in a morphologically and behaviorally feminine phenotype (Adkins-Regan 1981).

In both birds and mammals the homogametic sex typically exhibits philopatric behavior, while the heterogametic sex engages in natal dispersal (Greenwood 1980). We therefore suggest that natal dispersal might be caused physiologically in representatives of these taxa by organizational effects of gonadal steroids in members of the heterogametic sex. However we emphasize that this hypothesis should apply only for natal dispersal and not for the various other types (e.g., saturation dispersal, breeding dispersal) described in the literature (Greenwood 1980; Lidicker 1975, this volume).

When they are eventually elucidated by future investigators, the proximal and ultimate causes of dispersal will probably be found to vary together. Thus an organizational endocrine mechanism such as that described here might proximally cause natal dispersal only where natural selection has favored regular dispersal by one sex. Where the success of individuals depends on their ability to respond differentially to environmental variables, dispersal might be an inappropriate response to local conditions. Therefore a physiological mechanism that abolished or greatly reduced behavioral polymorphism would probably prove maladaptive. However, where sexually dimorphic dispersal behavior is consistently favored, selection might promote a metabolically efficient and relatively infallible mechanism such as organizational action of gonadal hormones on the developing nervous system.

We stress that the existence of such a mechanism would not preclude the operation (concurrent or otherwise) of other proximal factors in dispersal's causation. For example, it has long been suspected that resource shortages and/or social aggression promote natal dispersal in some birds and mammals (Dobson 1979, Greenwood and Harvey 1982, Lidicker 1975). In fact, it seems likely that such mechanisms must certainly operate if not regularly, then at least from time to time in many species. We suggest only that the endocrine mechanisms discussed here may operate in conjunction with other ontogenetic or ecological variables in the causation of natal dispersal.

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MIGRATIONS AND DISPERSAL OF BATS (CHIROPTERA)

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ABSTRACT

Information about the dispersal and migration of bats comes mainly from reports of seasonal appearances and disappearances of different species at specific localities, supplemented by some recoveries of banded individuals. Most data come from temperate populations in North America, Europe and Australia, but tropical evidence mainly from the Paleotropics concerns both frugivorous and insectivorous species. Migrations of bats in tropical and temperate zones coincide with seasonal changes in food supply, but in tropical communities some bat species are resident throughout the year. Recent studies of ***Myotis grisescens*** (Vespertilionidae) provide evidence of point-to-point migrations. Studies with ***Tadarida brasiliensis*** (Molossidae) indicate the importance of mortality associated with the stress of migration. Although band recovery data for many bats suggest a high level of roost fidelity and philopatry, genetic studies indicate considerable mixing of populations. In the case of ***Myotis lucifugus***, a random and promiscuous mating system and vagrancy of individuals during the breeding season seem to promote gene flow over large areas. Even species with more structured mating systems (e.g., some Phyllostomidae) show genetic evidence of dispersal.

INTRODUCTION

Flight gives bats along with birds the ability to move over considerable distances, whether migrating to exploit seasonal changes in resource distribution or dispersing to distant areas. The available data on the migrations of bats were reviewed by Griffin (1970) who considered evidence that pointed to seasonal movements (migrations) by several species. Migrations appear typical of many temperate and tropical species, both frugivores and insectivores. Despite the rapid increase in published information about bat ecology since Griffin's (1970) review, we have accumulated relatively little solid data on point-to-point movements of bats beyond occasional reports of recoveries of banded individuals. Some recent studies, however, have added to our knowledge about bat migration and dispersal.

The purpose of this paper is to consider new data on migrations and dispersal of bats which have accumulated since Griffin's (1970) review, without unnecessary duplication of his synthesis. We consider data from a variety of sources, including banding studies, investigations of communities of bats, and anecdotal evidence. We also consider how mating systems and genetic studies have produced results that bear on the question of mixing of populations of bats through dispersal. In this paper we define dispersal as the permanent movement of individuals, usually young of the year, away from the parental home range (equivalent to Baker's (1978) one-way migration). Migration signifies the seasonal round-trip movements of individuals between more or less distant sites.

CUES FOR ORIENTATION

A topic not addressed here in detail but one which is relevant to the general question of migrations of bats is the orientation cues that migrating bats may use. Bats, including some echolocating species, are capable of using a variety of cues including visual and non-echolocation acoustic cues while orienting within their normal home range (Buchler and Childs 1981, Childs and Buchler 1981). Given its short range of operation (Kick 1982), echolocation may be of limited value in long-range orientation. To date, however, there have been no studies of long-distance navigation in migrating bats, and most of the evidence for orientation cues comes from homing studies. Work with ***Phyllostomus hastatus*** (Phyllostomidae) involving radio-tracking individuals under varying degrees of sensory deprivation showed that these bats relied to some degree on vision to relocate their roost (Williams, Williams and Griffin 1966; Williams and Williams 1967). Visually deprived animals were slower to return home and used more circuitous routes. The relevance of most homing studies in providing evidence for long-distance orientation, however, is questionable since Wilson and Findley (1972) argued that all of the bat homing studies that they considered could be explained by random movements rather than directed homing. These studies, including those of *P. **hastatus***, are also complicated by the lack of knowledge of the home ranges of the animals under study. Indeed, data on home ranges or familiar areas are unavailable for most species.

An additional complication plaguing homing studies is the lack of a clear identification of "home." A review of patterns of roost use by different species of bats (Table 1) makes it clear that while some species predictably and repeatedly return to the same roost (in some cases for years), other species often change roost sites, sometimes on a daily basis. In some cases, roost switching may be a result of roost availability, e.g., the situation facing ***Thyroptera tricolor*** (Thyropteridae) whose roost sites in partially furled banana or ***Heliconia*** leaves are exploitable for only 24 hours (Findley and Wilson 1974). In others, the reasons for roost hopping are not clear, e.g., the vespertilionid ***Scotophilus leucogaster*** which moves among a number of continuously available roosts (Fenton 1983a).

Table 1
Patterns of day roosts by different bats.

Species	Roost Site	Study Technique	Roost Fidelity; Patterns of Movement between Roosts	Source
Pteropodidae				
Epomophorus gambianus (in Zimbabwe)	F[1]	rt[2]	frequent moves between adjacent but close trees	Thomas and Fenton 1978
Epomophorus gambianus (in Cote d'Ivoire)	F	rt	use of a variety of sites within a small area (300 m diameter)	Thomas 1982
Hypsignathus monstrosus	F	rt	shift between sites at short intervals	Bradbury and Vehrencamp 1977b
Epomops buettikoferi	F	rt	use same roost unless disturbed	Thomas 1982
Emballonuridae				
Rhynchonycteris naso	T[3]	rb[4]	3 to 6 roost sites, moves between them at intervals	Bradbury and Vehrencamp 1976
Saccopteryx bilineata	T	rb	use one roost for long periods	Bradbury and Vehrencamp 1976
Saccopteryx leptura	T	rb	set of roosts, move between them at intervals	Bradbury and Vehrencamp 1976
Phyllostomidae				
Carollia perspicillata	C/F[5]	rt	most bats consistently used one roost	Heithaus and Fleming 1978
Phyllostomus hastatus	C	rt	consistently used the same roost over 2 or 3 years	McCracken and Bradbury 1981
Vampyrum spectrum	H[6]	rt	used one roost	Vehrencamp et al. 1977
Vampyrodes caraccioli	F	rt	remained in same general area but used a range of roost sites, rarely used same roost two nights consecutively	Morrison 1980
Artibeus literatus	F	rt	as for *V. caraccioli*	Morrison 1980
Artibeus jamaicensis	H/F	rt	fidelity depended upon nature of roost, some moves between roosts	Morrison 1979
Vespertilionidae				
Eptesicus fuscus	B[7]	rt	frequent moves between roosts over large area (over 1 km diameter)	Gedggie 1983
Scotophilus leucogaster	H	rt	frequent moves between roosts from day to day over small area	Fenton 1983b
Antrozous pallidus	C	o[8]	frequent shifts from roost to roost	Vaughan and O'Shea 1976

[1] foliage; [2] radio-tracking; [3] tree trunk; [4] reflective band; [5] C-cave; [6] hollow tree; [7] building; [8] observation

Data on roost fidelity (Table 1) have important implications for studies of homing by bats. The failure of an individual to return to the roost from which it was removed could reflect the animal's response to disturbance and its choice of an alternate roost. Failure to return to the original capture site may tell nothing about the animal's ability to find home.

MIGRATION

The evidence for migration in bats comes primarily from the seasonal appearances and disappearances of bats from roosts, and to a lesser degree on recaptures of banded individuals. Work published since 1970 has not provided any major departures from these indirect data but has expanded the data base considerably.

Tropical Bats

Thomas (1983) conducted a two-year study of the seasonal changes in a community of fruit bats (Pteropodidae), mainly in Ivory Coast in west Africa (Fig 1). The primary study area was in southern Guinea savanna (Lamto), but he also sampled communities in Sudanese savanna (Wango Fitini) to the north and in high forest to the south (Tai Forest). Along this south to north axis (forest to dry savanna) the seasonal rainfall patterns are determined by the northward movement of the intertropical front into the savannas. This front brings rains in the March to June period, and the subsequent southward retreat of the front brings a second rainy season in September to November. Using observations and netting to monitor the seasonal changes in community composition, Thomas (1983) found that all three sites had some resident species, but three species (***Eidolon helvum***, ***Myonycteris torquata*** and ***Nanonycteris veldkampi***) showed striking complementary patterns of abundance between the sites.

During the dry season when they were absent from savanna sites, ***E. helvum*** roosted in at least one major colony (300,000500,000 individuals) in the forest zone (Abidjan). Following the birth of young in January and February, this colony declined rapidly to only a few hundred individuals during March to June and remained small until October. Concurrent with the apparent desertion of the forest colony, small scattered groups of males were found roosting in the savanna ***Borassus aethiopum*** palms to the north at Lamto. Between 12 (1980) and 14 (1979) days after the first males appeared at Lamto, about 100,000 males and females carrying non-volant young arrived overnight and formed a colony covering about 50 ha at Lamto. These bats remained only 45 days (1979) and 37 days (1980) and departed en masse in a single day. Following the departure from Lamto, a smaller colony (2,0005,000) appeared at Ferkessedougou to the north in April and remained there until the end of May. Again concurrent with the movement of this colony, Thomas (1983) found a few ***E. helvum*** at San to the north in Mali in July (Fig 1). After July there was no evidence of colony formation between San and Lamto, but netting at the latter site showed a major increase in abundance preceding a build-up in the Abidjan colony which reached its peak in December. Thomas (1983) concluded that ***E. helvum***

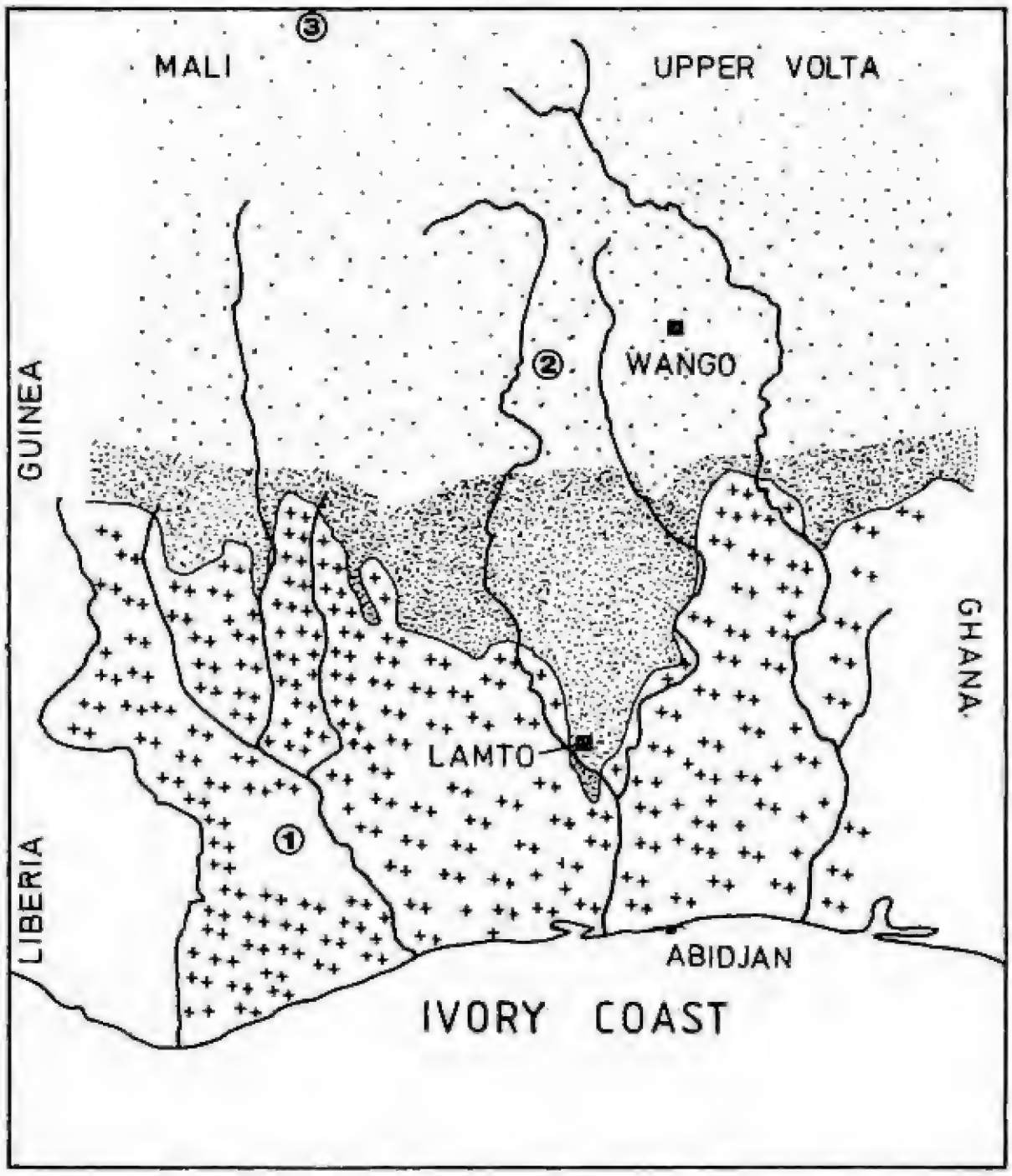


Figure 1

A map of part of west Africa showing the study locations at Abidjan, Lamto, Wango Fitini (Wango), Ferkessedougou (2), the Tai Forest (1), and San (3). High forest is represented by crosses, southern Guinea savanna by closely spaced stipples and southern Sudanese savanna by widely spaced stipples.

followed the movement of the rains into the Niger River basin, a flight of some 1500 km annually.

Seasonal changes in colony size of *E. helvum* have been documented throughout its range (Thomas 1983, and references cited therein). In east Africa, where north-south movements are not restricted by the coast, migrations may be considerably greater, and colonies of *E. helvum* fluctuate in size at either end of the continent (Sudan and South Africa). The links between colonies at the northern and southern extent of its range, however, remain unknown.

Two solitary species, ***M. torquata*** and ***N. veldkampi***, show minor variations in this pattern of movement. During the dry season (November to March) ***M. torquata*** was the most commonly captured species in the Tai Forest, but it was absent at that time from both Guinea and Sudanese savanna sites. As the intertropical front and rains progressed northwards into the southern Guinea savanna (March/April) and later into southern Sudanese savanna (April/May), capture rates increased sequentially in both habitats. ***Myonycteris torquata*** was first caught at Lamto in April and May and was the most commonly captured species in this community in June. It was rare or absent at Lamto in July and August. Twelve days after the first capture at Lamto, ***M. torquata*** appeared in southern Sudanese savanna to the north where the catch rate peaked in May and June before declining between July and October. With the subsequent retreat of the rains southward between July and November, catch rates first peaked at the southern Sudanese savanna site and then at Lamto. Thomas (1983) suggested the successive peaks in captures indicated that ***M. torquata*** moved through and beyond Guinea and southern Sudanese zones during the rainy season and then retreated to the forest during the dry season. Interestingly, this over 750-km round-trip migration into the northern savanna appeared (from capture data) to be restricted to pubertal and subadult males. These individuals may have moved into the savannas to exploit local super-abundances of fruits, while adult males and females tended to remain in the forest zone and peripheral savannas. Sex ratios of specimens of ***M. torquata*** in museum collections from other parts of its geographical range are consistent with a predominantly male migration.

Nanonycteris veldkampi exhibits a similar bimodal pattern of abundance at Lamto, but the timing of the single peak in the southern Sudanese site (Wango Fitini) to the north suggests that this species does not move beyond this zone. Thomas (1983) found no evidence of a sex bias in captures of *N.* ***veldkampi*** at either site, indicating that both males and females migrate the ca. 750 km annually.

Thomas (1983) concluded that the bats migrated to exploit wet season peaks of availability in fruit in the savanna zones but questioned why the species should leave the forest when there was a concurrent peak in fruit production there. He suggested that seasonality and changing population levels combine to foster competition which is partly resolved by migration. Interestingly, these bats may not be energy limited since they over-ingest energy daily by processing large amounts of protein-poor fruits (Thomas 1984). The energetic cost of migration, therefore, may be minimal to the bats, requiring only re-channeling of existing energy intake.

There are no startling new finds from pteropodids in other parts of the Old World. Nelson (1965) demonstrated that some seasonal changes in colonies of ***Pteropus poliocephallus*** in Australia constituted local movements from main camps to satellite locations rather than migrations over long distances. Prociv (1983) reported fluctuations in numbers of bats at camps of ***Pteropus scapulatus*** which were complementary over distances of 500 km and which he interpreted as evidence of migration in this species.

Vaughan (1977) documented seasonal changes in populations of the insectivorous ***Hipposideros commersoni*** (Hipposideridae) at different sites in Kenya. O'Shea and Vaughan (1980) reported data collected over one year at a site in Kenya which showed seasonal changes in faunal composition. Sampling with mist nets and traps, these authors encountered 25 species representing 7 families (10 Vespertilionidae, 6 Molossidae, 5 Rhinolophidae, and one each of Pteropodidae, Emballonuridae and Nycteridae: O'Shea and Vaughan treated the Hipposideridae as part of the Rhinolophidae). Only ten insectivorous species and one frugivore were present throughout the year; they found lower species richness and diversity during the dry season, a fact they attributed to emigration. O'Shea and Vaughan (1980) noted that areas within less than 500 km had complementary patterns of rainfall and suggested that the bats oscillated between these sites. They also found build-ups of subcutaneous fat in several species suspected of migration, including: ***H. commersoni***, ***Miniopterus natalensis***, ***Scotophilus nigrita***, ***Scotoecus hindei***, ***Tadarida condylura***, ***T. pumila***, ***T. bemmelini*** and ***Platymops setiger***. McWilliam (1982), however, found a good correlation between fat deposits and the demands of different mating systems in some east African bats, and the fat reported by O'Shea and Vaughan (1980) may not have been used for migration.

We have similar data from a community of bats in Zimbabwe where seasonal changes in the composition of the bat community coincided with the rainy season. Some species, e.g., ***Otomops martiensseni*** (Molossidae) which is easily monitored via its loud and audible (to man) echolocation calls (Fenton and Bell 1981), do not occur in mopani and miombo woodland during the wet season, apparently arriving there at the end of the rains and leaving again before the rains begin.

It is interesting and perhaps significant that studies of neotropical communities of fruit bats (Phyllostomidae) have produced little evidence for migrations. Bonnacorso (1979) and Humphrey and Bonnacorso (1979) documented important seasonal changes in food availability over one year at Barro Colorado Island (Panama) but paid little attention to the role of migration in the community of phyllostomid bats. Bonnacorso (1979) noted that some species appeared to be absent from Barro Colorado Island in some seasons but presented no real case for migration. Humphrey and Bonnacorso (1979) refer only to data from some nectar feeders from the American southwest in considering evidence for migration in the Phyllostomidae. Other workers have found the data on the seasonal abundances of these nectar-feeders and the flowers they visit more convincing (e.g., Fenton and Kuntz 1977, Howell 1979). However, the lack of either recaptures of marked individuals or obvious complementary changes in populations at different locations mean that evidence for migration is at best circumstantial.

Although some species in tropical situations from forest to savanna show seasonal changes in abundance, often providing strong circumstantial evidence for migration, other species are more sedentary (e.g., O'Shea and Vaughan 1980, Thomas 1983). Some resident bats adjust their patterns of food consumption to the prevailing conditions (e.g., Advani 1981), others may pass long inclement periods by aestivation (Brossett 1966). Long-term investigations of both bats and their food supplies are

needed to elucidate the details of bat migrations in the tropics. Ongoing work on the fruit bat communities in Australia (G.C. Richards, personal communication) and elsewhere promise to provide more details in the relatively near future.

Temperate Bats

There have been two important developments in the study of migration by temperate bats since Griffin's (1970) review. Tuttle (1976) reported a detailed study of the migrations of the vespertilionid ***Myotis grisescens***, and others, including Tuttle, have provided data about migration as a mortality factor in bats (Geluso, Altenbach and Wilson 1976; Tuttle and Stevenson 1977).

Tuttle (1976) banded 19,817 ***M. grisescens*** over several years and from this population obtained 11,133 recoveries. Adults showed higher rates of recovery than subadults. The bats were strongly philopatric to maternity caves, although they sometimes roosted in several caves within their home ranges. Band recovery data which included a number of individual round trips between summer and winter caves indicated that bats tended to hibernate in caves where they had spent their first winter. The bats invariably spent the summer in warm caves and the winter in cold caves (hibernacula). Movements between the two types of locations involved one-way distances of 17 to 437 km and occurred in the spring and fall. The migration routes between caves were not always the most direct, being longer apparently to provide access to caves en route. Tuttle (1976) found definite patterns of arrival and departure according to sex and age. The bats showed variable rates of travel, in some cases moving 20 $km \cdot h^{-1}$ and covering 15 to 52 km per night. Tuttle (1976) used sampling of populations (as opposed to data from individuals) to establish that greater migration distances positively correlated with greater weight loss.

Tuttle's (1976) data provide a relatively complete picture of the migratory biology of ***M. grisescens***, making our knowledge of these movements comparable to the situation for the molossid ***Tadarida brasiliensis*** (Davis, Herreid and Short 1962; Griffin 1970). These two data bases could only be improved by further work on the precise movement patterns of individuals. Although bats with body masses of $\geq$ 20 g can now be studied by radio-tracking, neither ***M. grisescens*** nor ***T. brasiliensis*** is large enough to carry even 0.9 g transmitters, and with ranges of about 1 km these small instruments are not suitable for studies of the paths of migrating bats.

Building on data accumulated about the migrations of ***T. brasiliensis*** in the American southwest and adjacent Mexico, Geluso et al. (1976) demonstrate how migration led to increased levels of mortality in this species. Mortality usually involved young of the year and resulted from the metabolism of accumulated body fat and subsequent release of toxic levels of DDT, DDE and DDD. These data and those of Tuttle (1976) suggest that during migration the bats relied heavily on body fat, implying that the animals did not feed substantially during migration.

MIGRATION, DISPERSAL AND GENE FLOW

As mentioned earlier, we consider dispersal as the permanent movement of individuals away from the parental home range. Such movements can enhance gene flow within and between populations, so dispersal has important implications in the population biology of species, especially sedentary ones. For bats, however, the distinction between migration and dispersal is often clouded by the nature of seasonal movements made by individuals between different roost types. In temperate zone bats, movements between nursery colonies, fall roosts, and winter hibernation sites represent round-trip migrations for most individuals. Some proportion of the population, however, may not return to the same nursery colony in successive years, and this may represent dispersal. To what extent this dispersal is real (not an artifact of banding disturbance) and contributes to genetic mixing across the range of temperate species such as ***Myotis lucifugus*** is not clear at this time. Currently, there are no satisfactory data on dispersal of any bat species.

Data on dispersal of bats are generally inferred from banding studies. Band recoveries, however, may or may not be an accurate means of defining movements. From recovery of banded individuals several authors (e.g., Barbour and Davis 1969) have suggested that the vespertilionid ***Eptesicus fuscus*** is a sedentary species. Recently, Brigham (1983) used radio-tracking to follow the movements of 38 individuals (total of 229 bat-days). His data which cover the period of May to September suggest that the animals are indeed roost-loyal and sedentary. Another study (Geggie 1982) provided some evidence of roost-switching by ***E. Fuscus***, but none of the movements were over long distances. Accepting that Brigham's data may not have spanned an important dispersal period, they still provide preliminary confirmation of band data. There is, however, no similar "calibration" of the band recovery data for ***M. lucifugus***.

In their study of ***M. lucifugus***, Humphrey and Cope (1976) arbitrarily defined migrations as the movements of individuals from summer nursery colonies to hibernation caves, and dispersal as all other movements. Since ***M. lucifugus*** visits a variety of roost sites prior to entering the hibernation caves, these movements do not necessarily represent permanent movements from the parental home range.

On the basis of band recapture data from their own and other studies, Humphrey and Cope (1976) identified several demes (defined as a "functional unit whose distribution is defined...a distinct population of interbreeding animals," p. 62) in populations of ***M. lucifugus*** in eastern North America. If the band recoveries accurately portray the extent and limits of dispersal movements, then colonies should be genetically similar within demes and genetically dissimilar between demes.

Carmody, Fenton and Lee (1971) used electrophoretic techniques to compare three hibernating populations of ***M. lucifugus*** in southern Ontario (Fig 2). Fenton (1969) had previously reported the movements of two banded males between hibernation caves 1 and 3, and 4 and 3 (Fig 2). Bats known to hibernate at sites 2, 3 and 4 had also been recovered at a single nursery colony (inverted triangle in Figure 2) and Humphrey and Cope (1976) recognized this area as defining one deme. The

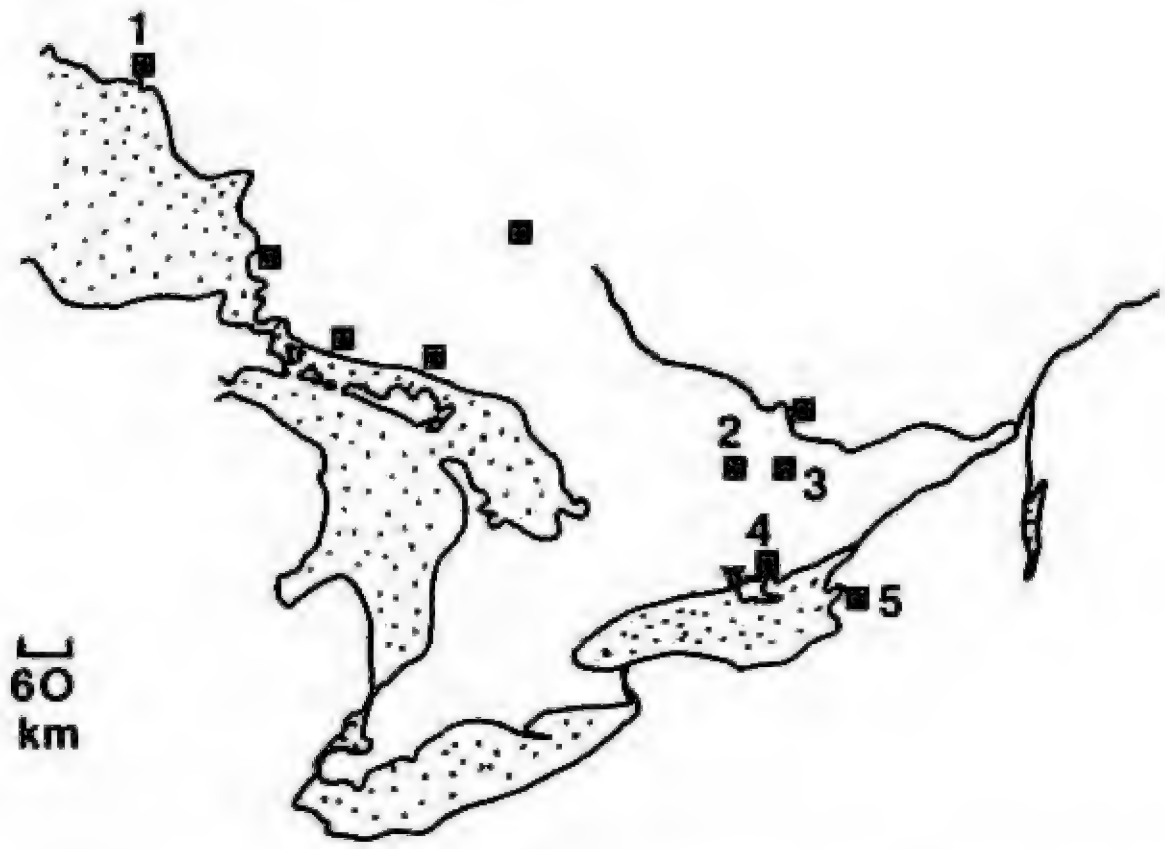
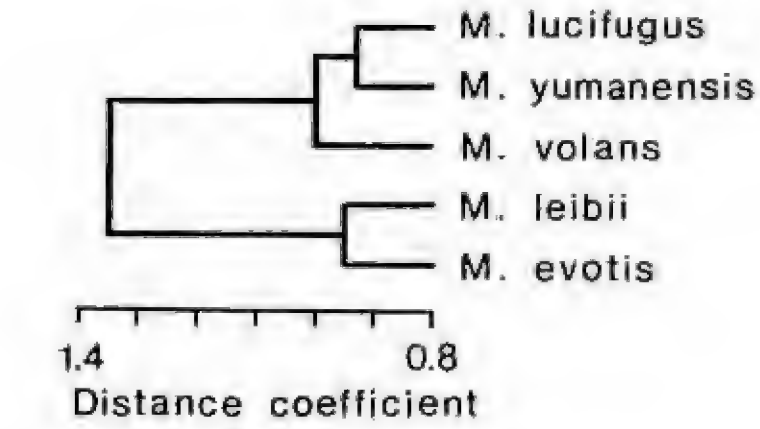


Figure 2

A map of the Great Lakes of eastern North America showing the locations of hibernacula (boxes) and one summer colony (triangles) used by *Myotis lucifugus*. Sites 1, 2, 3 and 5 have been used to obtain bats for genetic studies (Carmody et al. 1971, Herd 1983), and bats banded at hibernacula 2, 3 and 4 have been recovered at the summer colony (Fenton 1970).

three hibernating populations showed no evidence of genetic isolation, consistent with the evidence based on movements. In a more extensive electrophoretic study, however, Herd (1983) and Herd and Fenton (1983) found no evidence of genetic isolation between populations of ***M. lucifugus*** as widely separated as the Okanagan Valley of British Columbia and Ontario (Fig 3). These data suggest considerable gene flow across the range of ***M. lucifugus*** in northern North America and cast doubt on the validity of demes as defined by band recoveries.

Until it is possible to distinguish dispersing from migrating individuals, it will be impossible to know the contribution of dispersal to this apparently high gene flow. Probably three factors, true dispersal of individuals to new areas, the timing of mating with respect to seasonal migrations to hibernation sites, and the mating system of ***M. lucifugus***, together enhance gene flow between populations. During the latter part of the summer, from August until frost, ***M. lucifugus*** is vagrant, moving to different locations, swarming at hibernacula (Fenton 1969) and visiting different nursery colonies (Humphrey and Cope 1976). The late summer and early autumn swarming at hibernacula involves adults and subadults of both sexes, and this is the time when most long distance band recoveries have been noted. In Ontario, mating begins in the middle of August and peaks at the beginning of September coincident with swarming and the period of considerable movements. These movements, whether technically migration or dispersal, result in maximal mixing of populations during mating. Interestingly, Thomas, Fenton and Barclay (1979) found that the mating system of ***M. lucifugus*** was random and promiscuous, apparently determined by the inability of



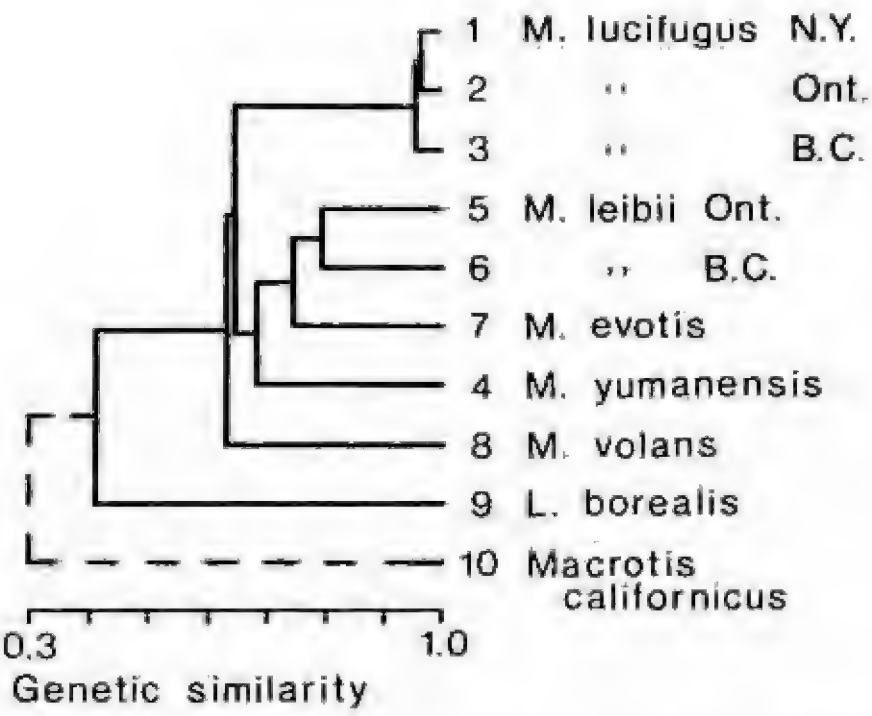


Figure 3

Genetic distance and similarity between several species of Canadian bats. See text for details.

either sex to protect its investment in mate choice. Such a mating system must increase the probability that migrating or dispersing individuals will successfully mate and make genetic contributions to local populations.

Unfortunately since we lack equivalent genetic and mating systems data for other temperate species such as ***E. fuscus*** and ***M. grisescens***, it is impossible to determine the incidence of the ***M. lucifugus*** pattern of genetic mixing. One set of genetic data from a tropical species, the phyllostomid ***Uroderma bilobatum***, suggests that the situation in ***M. lucifugus*** is not typical of bats in general. Several studies (e.g., Baker, Bleier and Atchley 1975; Baker 1981; Greenbaum 1981; Hafner 1982) have identified a contact zone between two karyotypically distinct subspecies of ***U. bilobatum***. Although Baker (1981) and Greenbaum (1981) proposed that this contact zone was unique in a number of ways, notably its great width (400 km), Hafner (1982) has challenged these conclusions and maintains that the hybrid zone is narrower (35 km) and within the range reported for similar zones in other taxa. Either interpretation suggests a level of genetic isolation contrasting with the data for ***M. lucifugus***.

There are no data about the mating system of *U. **bilobatum***, but harem defense polygyny is common among other phyllostomids (Bradbury 1977a). In some cases (***Phyllostomus hastatus***) harem males sire up to 95% of the young born in their harems (McCracken and Bradbury 1977). Harems are known from some other phyllostomids (Porter 1979; Kuntz, August and Burnett 1983; Vehrencamp, Stiles and Bradbury 1977) where they seem more stable than those reported from some emballonurids (Bradbury and Emmons 1974). Porter and McCracken (1983), however, showed by genetic analysis that harem male ***Carollia perspicillata*** (Phyllostomidae) cared for young that were not theirs, so harem defense polygyny is not necessarily a genetically "tight" situation (cf. Wilson, Bush, Case and King 1975).

We suggest that the evidence from genetic studies, movements of banded individuals and the mating system in ***M. lucifugus*** indicate a level of genetic mixing of populations which is not compatible with the deme model proposed by Humphrey and Cope (1976). Species with more structured mating systems (—more skewed male contributions) may show more evidence of genetic isolation, but the data base for bats in general is too meager to permit broad generalizations, and genetic mixing of even chromosomally distinct populations occurs (Hafner 1982).

The importance of migrations and dispersal in the lives of bats pervades several facets of their biology. In one setting, flight permits them to colonize otherwise isolated areas such as oceanic islands. Periods of the year, whether long or short, when individuals are vagrant, particularly when they occur during the mating season, can completely neutralize high levels of philopatry. Banding studies permit only a general identification of basic patterns of movement, and details about the behavior of individuals are necessary to document patterns of movements and to distinguish dispersal from migration.

Circumstances may lead to remarkable dispersal by bats. Fenton (1983b) reported that undetermined numbers of ***M. lucifugus*** moved from Dalhousie, New Brunswick, in eastern Canada to Rotterdam in Holland and perhaps to Southampton in England. The bats used a vessel that loaded forest products in Dalhousie as a night roost and were carried by it to the ports in Europe. Movements appear to have covered two summers, but there are no data about the success of this dispersal to another continent.

We still have a great deal to learn about the dispersal and migrations of bats.

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SEX-SPECIFIC DYNAMICS OF AGGREGATION AND DISPERSAL IN REPTILES AND AMPHIBIANS

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ABSTRACT

A model of sex-specific dynamics of aggregation and dispersal is presented. The model introduces a dispersal analog of the demographer's marriage dominance function. Simulation analysis shows that for species such as many amphibians and reptiles, males will respond to changes in the spatial pattern of the environment by moving more readily than females. Data from three-toed box turtles (*Terrapene carolina triunguis*) are analyzed in terms of this model and in terms of their relevance to the problem of the evolution of sex ratio in turtles.

INTRODUCTION

Many species of amphibians and reptiles undergo seasonal cycles of aggregation for breeding followed by dispersal. In addition in temperate climates many species show seasonal cycles of aggregation and dispersal for hibernation or aestivation. In this paper I investigate the sex-specific dynamics of such bouts of aggregation and dispersal. A model of sex-specific movement patterns is introduced following the methodology of Kiester and Slatkin (1974), but with the addition of a movement pattern analog of the marriage dominance functions of two-sex demographic dynamics. Qualitative properties of the model are presented which show differences between the sexes in response to a change in the environment or to a seasonal necessity such as hibernation. The model is then applied to seasonal fluctuations in the numbers of box turtles, and this application is further analyzed in terms of the problem of the evolution of sex ratio in turtles.

Migration and Dispersal in Amphibians and Reptiles

At the substanstial risk of over-simplifying the life history patterns of two entire Classes of vertebrates, I will describe three general patterns of aggregation and dispersal in amphibians and reptiles.

The first, which I will call the "classical pattern," is where both sexes seasonally aggregate at patchy breeding sites for both mating and egg laying. The adults then disperse after breeding, while the young disperse after reaching a given age. This pattern is shown by many frogs and salamanders and is, of course, the one presumed to be the case for the original species of amphibians which colonized the land.

The "neo-classical pattern" is an important extension of the original pattern. Here mating may take place at various distances away from the actual site of egg deposition. Among recent reptiles the most spectacular cases are the sea turtles. For the Ridley turtle (***Lepidochelys kempi***) something like the entire Caribbean population breeds on a single beach in a few nights (Carr 1963).

Finally the "modern pattern" has both dispersed mating and dispersed egg deposition (or parturition for ovoviviparous species). This pattern occurs for most lizards and snakes but also for those terrestrial salamanders that have evolved live-bearing reproduction (Taylor and Guttman 1977; Huey, Pianka and Schoener 1983).

Aggregation for hibernation occurs for those species which have specific requirements for hibernacula which are patchily distributed. The most spectacular example is the red-sided garter snake (***Thamnophis sirtalis parietalis***) in Canada. Aleksiuk (1976) found "... as many as 5,000−8,000 may use a given hibernaculum." Brown and Parker (1976) found several hundred racers (***Coluber constrictor***) utilizing a den in Utah. Many other species of snakes as well as terrestrial turtles seasonally aggregate for hibernation. From the point of view of the spatial dynamics of mating, this pattern of seasonal aggregation and dispersal has a similar effect to that of the neoclassical pattern of reproduction, in that mating may occur as aggregation or dispersal takes place.

Types of Dispersal Models

Many types of mathematical models of dispersal or migration have been proposed (Endler 1977, Horn 1983). While a complete review of the various kinds of models would be desirable, the field has probably not stabilized enough to allow such an undertaking. Some distinctions between kinds of models are worth noting, however. First, we may distinguish genetic models which monitor genes and genotypes (and possibly individuals) from non-genetic models where only individuals are counted. Second, we may contrast demographic models with behavioral models: the former concern the locations of individuals only at their times of birth and reproduction, whereas the latter track the location of individuals more or less continuously. Finally, we may distinguish what can be called adjacency models from non-adjacency models. An adjacency model is one in which the decision an animal

makes to move some relatively short distance is assumed to depend only on a comparison of nearby available environments for which the animal can develop some immediate knowledge. In non-adjacency models, animals are assumed to make decisions to move not just on the relative merits of nearby localities, but on the basis of environmental cues valid for long distances, memory, and genetic predisposition as well. Non-adjacency models obviously are needed for such phenomena as long distance migration but ultimately will be required for a complete understanding of any species with more complex behavior.

The purpose of this paper is to help understand the sex-specific dynamics of the patterns of movement that occur during aggregation or dispersal for either the neoclassical pattern of reproduction or the use of dispersed hibernacula. In both cases, mating can occur as the individuals move, and therefore these dynamics will directly influence the patterns of mating in the population through time. The question is: how might the two sexes differentially evolve strategies of movement for use during these cycles? Bateman (1948) showed that on the whole, males have a greater variance in reproductive success than females. We might therefore expect that the evolution of different male and female movement patterns would be consonant with this overall pattern.

THE MODEL

The model proposed here is a generalization to two sexes of the movement pattern model presented by Kiester and Slatkin (1974). It assumes a fixed number of individuals of each sex. These individuals move about in response to changes in the level of resources and in the numbers of each sex. Individuals are postulated to assess the relative merits of neighboring patches and their current patch and either to move to one of the neighboring patches or to stay put. Sex-specific differences are introduced through functions which describe the relative weights given by members of each sex to members of each sex when assessing patch value. In particular, if we take K as the carrying capacity, then the model assumes that individuals will tend to move into areas where the difference between the carrying capacity and the weighted (by sex) number of conspecifics is greater. This weighting function is the movement pattern analog of the the marriage dominance function used in two-sex demographic models such as the Kendall-Goodman equations (Kendall 1949, Goodman 1953) which weight the sex-specific effects on reproduction in a population (see Keyfitz 1968). Letting $E_m(i,t)$ and $E_f(i,t)$ be the merit or value of a location i at time t to a male and a female respectively, R_m and R_f be the sex-specific weighting functions for males and females, and $M(i,t)$ and $F(i,t)$ be the numbers of males and females in patch i at time t we have

$$E_m(i,t) = K(i,t) - R_m\,[M(i,t),F(i,t)] \tag{1}$$

$$E_f(i,t) = K(i,t) - R_f\,[M(i,t),F(i,t)] \tag{2}$$

The R functions can have many forms similar to the many possible forms of marriage

dominance functions. Perhaps the simplest case is given by the sex-specific differential weighting of the sum of the numbers of the sexes:

$$R_m = \gamma_{MM} M + \gamma_{MF} F \tag{3}$$

$$R_f = \gamma_{FM} M + \gamma_{FF} F \tag{4}$$

with all γ constants.

The simplest case is where each sex weights the members of both sexes equally so that

$$\gamma_{MM} = \gamma_{MF} = \gamma_{FM} = \gamma_{FF} = 1 \tag{5}$$

$$R_m = M + F = N \tag{6}$$

$$R_f = M + F = N. \tag{7}$$

Thus this case reduces to the single sex case. Much more interesting are the cases in which each sex weights the two sexes differently. In what follows we shall assume that

$$\gamma_{MM} = \gamma_{FM} = \gamma_{FF} = 1 \tag{8}$$

$$\gamma_{MF} = -1 \tag{9}$$

so that

$$R_m = M - F \tag{10}$$

$$R_f = M + F \tag{11}$$

and hence

$$E_m = K - M + F \tag{12}$$

$$E_f = K - M - F. \tag{13}$$

This particular version of the model assumes that females respond to the difference between the carrying capacity and the total number of conspecifics, that is, to the total amount of excess resource available. Males on the other hand are assumed to respond to the difference between the carrying capacity and the number of males as well as to the total number of females. Put another way, females are responding to the environmental resources available, whereas males are responding to the resources available and are also considering females as another type of resource. This situation may be called female movement dominance in analogy to female marriage dominance of demography. (Recall that "dominance" in this context does not imply any behavioral relations, only which sex is determining the dynamics to the greater extent.)

With a description of how each sex evaluates a patch in hand, we can now derive the dynamics of the movements of a population using the method of Kiester and Slatkin (1974). We model the environment as a discrete one-dimensional array of small patches. Each patch contains a value of K, and a number of males and females. Each animal is assumed to be able to estimate the value of the discrete patch it is in and that of the patch to the left and the patch to the right (that is, a total of three patches). Time is considered to be discrete as well. The number of, say, females in patch i at time $t + \Delta t$ is then equal to the number of females that were there at time t

plus the number that come in from the left patch (or minus the number that go out to the left patch) plus the number that come in from the right patch (or minus the number that go out to the right patch). The number that cross a boundary is proportional to the difference between the value of the two patches times the number of females in the patch that is being left. The patch that is being left is the one with the lower value and this determines the direction of movement in or out of a given patch. Thus if $m_r(i)$ is the net number of males and $f_r(i)$ is the net number of females which enter or leave patch i from the right and $m_l(i)$ and $f_l(i)$ are the net numbers which enter or leave from the left, then the model can be written as

$$M(i,t+\Delta t) = M(i,t) + m_r(i) + m_l(i) \tag{14}$$

$$F(i,t+\Delta t) = F(i,t) + f_r(i) + f_l(i) \tag{15}$$

with

$$m_r(i) = P\ M(i,t)\left[E_m(i) - E_m(i+1)\right] \quad E_m(i+1) > E_m(i) \tag{16}$$

$$= P\ M(i+1,t)\left[E_m(i) - E_m(i+1)\right] \quad E_m(i+1) < E_m(i) \tag{17}$$

$$m_l(i) = P\ M(i,t)\left[E_m(i) - E_m(i-1)\right] \quad E_m(i-1) > E_m(i) \tag{18}$$

$$= P\ M(i-1,t)\left[E_m(i) - E_m(i-1)\right] \quad E_m(i-1) < E_m(i) \tag{19}$$

$$f_r(i) = P\ M(i,t)\left[E_f(i) - E_f(i+1)\right] \quad E_f(i+1) > E_f(i) \tag{20}$$

$$= P\ M(i+1,t)\left[E_f(i) - E_f(i+1)\right] \quad E_f(i+1) < E_f(i) \tag{21}$$

$$f_l(i) = P\ M(i,t)\left[E_f(i) - E_f(i-1)\right] \quad E_f(i-1) > E_f(i) \tag{22}$$

$$= P\ M(i-1,t)\left[E_f(i) - E_f(i-1)\right] \quad E_f(i-1) < E_f(i) \tag{23}$$

where P is a proportionality constant which measures an individual's tendency to move given a difference in E values. This system of two coupled difference equations describes the movement of a population for a given initial distribution of males and females and a known pattern of spatial and temporal variation in the carrying capacity.

As developed in Kiester and Slatkin (1974), these equations can be approximated by their corresponding partial differential equations which for the model considered here would be

$$\frac{\partial M(x,t)}{\partial t} = -P\left(\frac{\partial}{\partial x}\right)\left(M(x,t)\frac{\partial}{\partial x}\left[K(x,t) - M(x,t) + F(x,t)\right]\right) \tag{24}$$

$$\frac{\partial F(x,t)}{\partial t} = -P\left(\frac{\partial}{\partial x}\right)\left(F(x,t)\frac{\partial}{\partial x}\left[K(x,t) - M(x,t) - F(x,t)\right]\right) \tag{25}$$

Analytical results for this continuous system will be presented elsewhere. For now, we revert to the difference equation system and study its qualitative dynamical properties using simulations.

SIMULATION OF THE MODEL

Simulations of the difference equation system were constructed for an array of 100 patches. Initially each patch contained 10 individuals of each sex and the carrying capacity was set to a given spatial pattern that did not vary temporally (see below). The constant P, measuring the tendency of an individual to move, was taken to be 0.01. Simulations were run for 24,000 time steps. All calculations were done with 64 bit precision. A copy of the source code is available from the author.

Results of Simulations

Three spatial patterns for the carrying capacity were simulated. The figures show the spatial pattern of the carrying capacity chosen for each simulation with the horizontal axis representing the value of the carrying capacity in arbitrary units. The first pattern ("ramp") is given in Figure 1a. Here the environment is constant at either end and increases linearly to a peak in the middle. Figure 1b shows the distribution of males and Figure 1c the distribution of females at times $t = 6000$ and $t = 24000$. Note that males have moved in to a much sharper, higher concentration than females. Figure 2a shows the second environmental pattern ("exp") which consists of centered back-to-back exponentials. Figures 2b and 2c show that males moved in to an even sharper concentration over the resource high point. Figure 3a shows the final pattern ("step") in which the environment is constant at a lower level at either end and then constant at a higher level in the middle with a discontinuous break. Figures 3a and 3b show that females move on to this resource high faster than do males, but that both sexes tend to have the same spatial pattern.

DISCUSSION

The results of these simulations show that for the case of female movement dominance, males respond more rapidly, converging faster onto new resource highs than do females. Moreover, males become more concentrated on the center of the resource high, whereas females remain more evenly distributed. That is, the response time of males is faster. An exception occurs when the variation in the environmental resource is discontinuous, but this may be biologically unreasonable since most animals can move enough to cross discontinuities. Although results of simulations creating only aggregations were presented, the same qualitative result holds for dispersal away from a disappearing resource high as well: males will depart more rapidly than females. Thus in a temporally variable environment, males will move about more than females. For the case of aggregation, a wave of advance of females moves onto the resource high at a relatively slow rate, while a higher and faster moving wave of advance of males moves through the wave of females. One result of this pattern of dynamics is that individual males encounter a greater number of different females than would be the case if both sexes responded similarly.

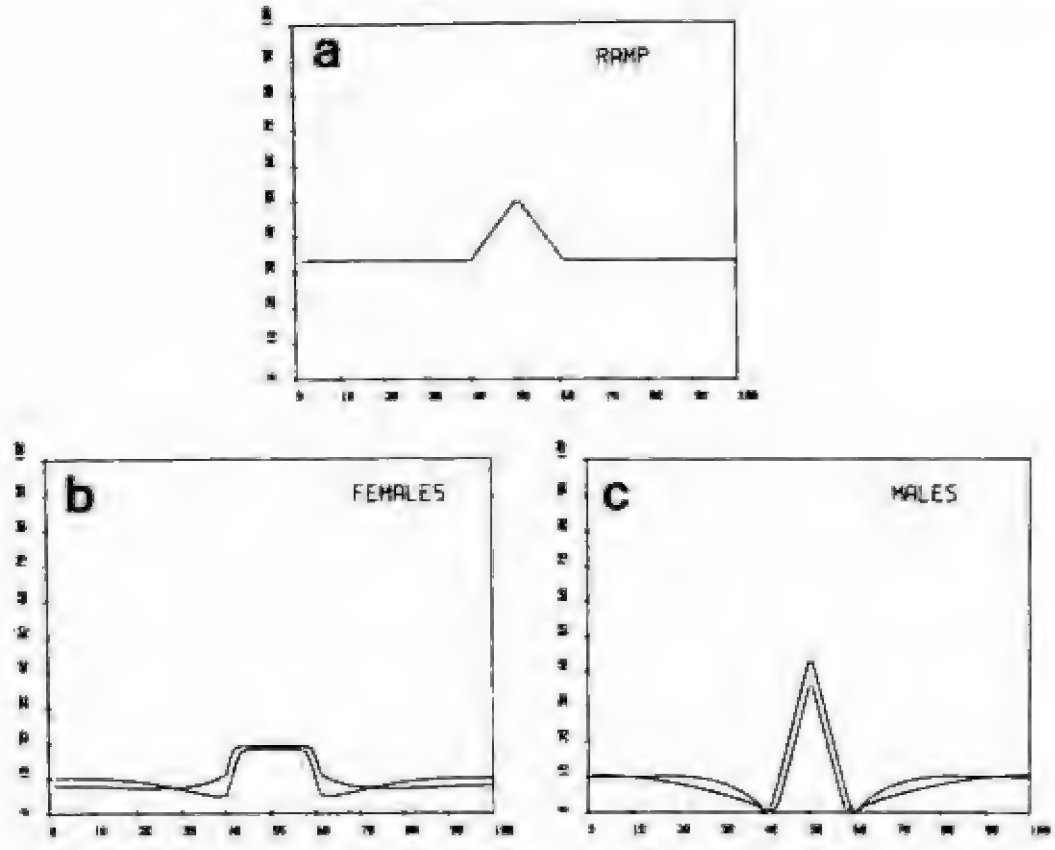

Figure 1

a) Arbitrary ramp pattern of spatial environmental variation. This pattern of resource distribution is assumed to come into existence at time $t = 0$. b) Distribution of males after 6000 (lower curve) and 24000 (upper curve) time steps. c) Distribution of females after 6000 (lower curve) and 24000 (upper curve) time steps.

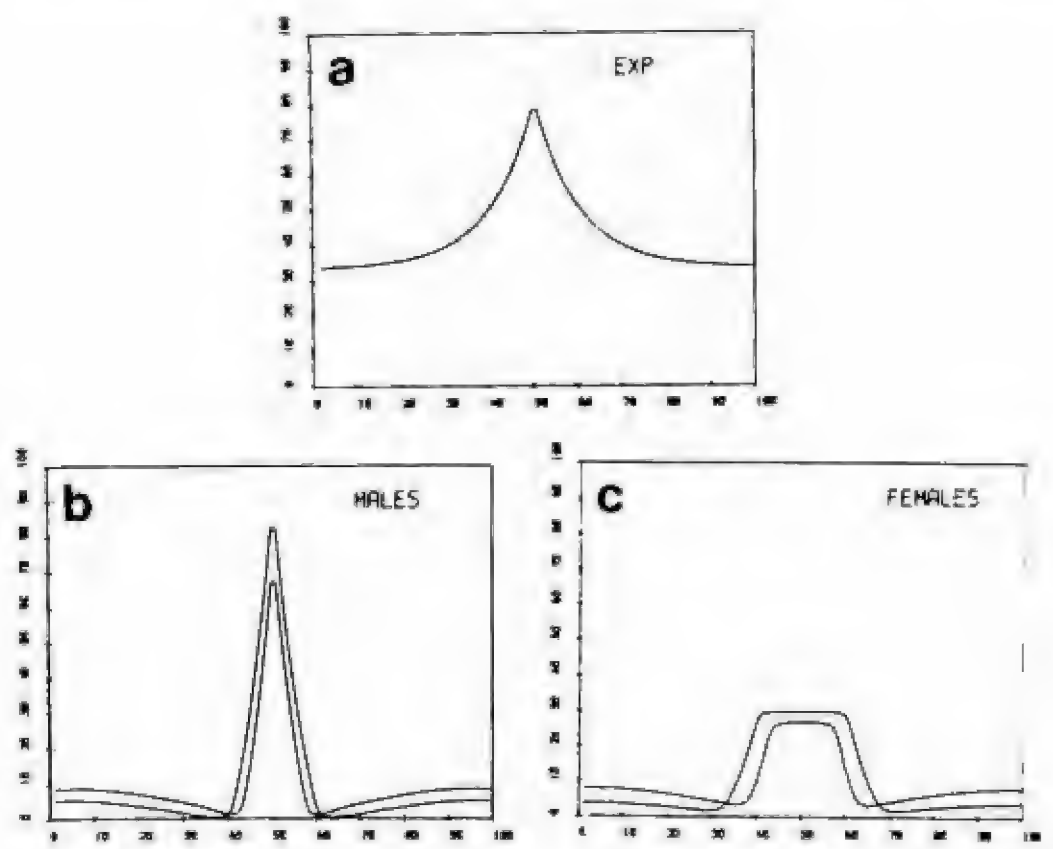

Figure 2

a) Pattern of spatial environmental variation consisting of back-to-back exponential curves. b) Distribution of males after 6000 (lower curve) and 24000 (upper curve) time steps. c) Distribution of females after 6000 (lower curve) and 24000 (upper curve) time steps.

This pattern of dynamics affects the pattern of mating for a species that mates promiscuously during cycles of aggregation and dispersal to and from either mating or hibernating sites. Many species of reptiles and amphibians may meet the assumptions of this model.

For example, three-toed box turtles (*Terrapene carolina triunguis*) hibernate in selected areas of good soil and cover. In the spring they disperse away from these areas and return to them again in the fall. During the active season there is a great deal of variability in the amount of movement that individuals undergo. Most remain in home ranges of various size, while a few are transients that move more or less continuously in one direction (Kiester, Schwartz and Schwartz 1982). This species mates promiscuously and appears to have female marriage dominance. In a nineteen year study of the population dynamics and movement patterns of this species in central Missouri, Schwartz, Schwartz and Kiester (1984) found sex-specific differences in demographic parameters. In addition, the data show sex-specific differences in movement patterns. In this study 1505 turtles were captured and recaptured a total of 6502 times. For each successive capture the distance from the previous capture was computed (the difference in the lengths of time between captures was ignored since the average time between captures was long enough to permit several recrossings of an area. Mean values for males and females for these distances were not different $t = 0.0077$, d.f. = 4395, not significant). However, the variance in distance moved was greater for males than females: $F = 1.10$, $\nu_1 = 2296$, $\nu_2 = 2099$, $p < 0.02$). Thus males are more variable in distance moved than females. This method does not include movements of individuals who were just passing through the study area since they are not recaptured. Known transient individuals are male, so this method may underestimate male movements.

This model and these empirical results may have a bearing on an outstanding problem in turtle biology: the control of sex ratios in natural populations. Many species of turtles possess a temperature dependent sex determination mechanism (Vogt and Bull 1982). While there may be some geographic variation in the response (Bull, Vogt and McCoy 1982) and some weak polygenic sex determination as well (Bull, Vogt and Bulmer 1982), it is still not clear how relatively even adult sex ratios are achieved in natural populations given that environmental variation could skew sex ratios in one direction or the other. Variation in female nest site choice may play a role (Vogt and Bull 1982). Sex-specific differences in movement pattern strategies may also be important. If one sex responds more rapidly to changes in the relative numbers of the sexes (for a given level of environmental resources), then individuals moving out of subpopulations with skewed sex ratios will effectively even out the population-wide sex ratio over time. High dispersal rates are thought to stabilize population numbers (den Boer 1968, Hastings 1982). In a similar manner they may stabilize long term effective sex ratios.

Bulmer and Taylor (1980) have argued that evolution will favor a sex ratio bias toward the sex which disperses more widely or more evenly. Turtle sex ratios are usually (but not always) female biased (Vogt and Bull 1982), and the model presented here shows that they will usually disperse more evenly. To understand the evolution

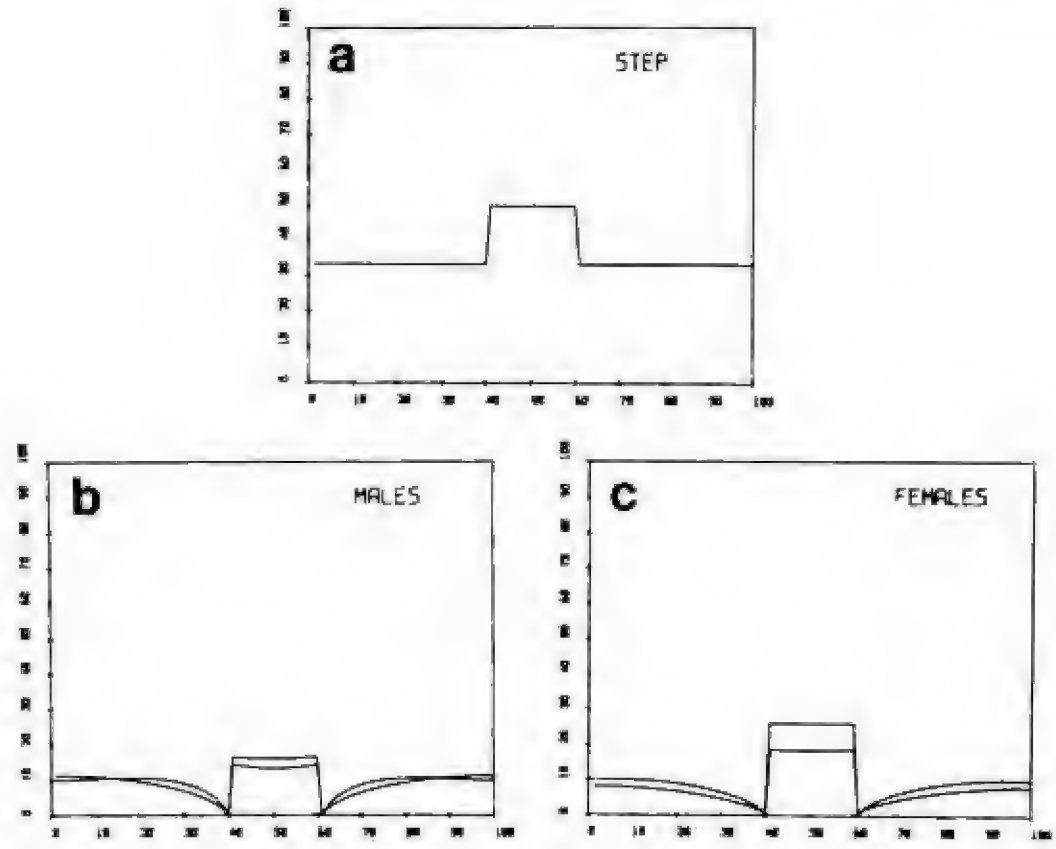

Figure 3

a) Pattern of spatial environmental variation consisting of a discontinuous step. b) Distribution of males after 6000 (lower curve) and 24000 (upper curve) time steps. c) Distribution of females after 6000 (lower curve) and 24000 (upper curve) time steps.

of sex ratios in turtle populations it will therefore be necessary to analyze the evolution of sex determination, sex-specific movement pattern strategies, and mating systems taken together. All of these aspects of turtle biology are components of a syndrome that characterizes animals like turtles, and they must be studied as a whole. Elton (1930) developed an analogy between dispersal and sexual recombination. The two may be even more intimately related than he thought.

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SEASONAL MIGRATION AND NESTING SITE FIDELITY IN THE GREEN IGUANA

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ABSTRACT

The seasonal migrations of female green iguanas (*Iguana iguana*) to nesting clearings on small islands around Barro Colorado Island in Panama were investigated using mark-recapture and radio-telemetry techniques. Although iguanas explored and occasionally nested in new clearings that became available during this study, our recapture results indicate that once iguanas locate a suitable nesting site, they usually return to nest there year after year. Female iguanas appear to nest annually upon reaching sexual maturity. Radio-tracking of iguanas as they moved away from one nesting site demonstrated that the lizards moved only moderate distances away from the site and always remained along the lake shoreline. Two iguanas were followed in successive years, and each returned to the same general vicinity each year, which suggests they were returning to established home areas. Because nesting sites are scarce and widely separated in this area, the limited movements and nesting site fidelity of the female iguanas may be contributing to a genetic structuring of their population.

INTRODUCTION

Green iguanas (*Iguana iguana*) are large, arboreal Neotropical lizards. Although the species has broad ecological tolerances and is widely distributed, it has rather specific nesting requirements. Unlike most tropical lizards (Fitch 1970), iguanas have a restricted annual breeding season. Nesting usually occurs during the dry season (Rand and Greene 1982), and the incubating eggs apparently must be laid in clearings that receive direct sunlight and have soils suitable for burrowing in to the proper depths (Licht and Moberly 1965, Rand 1972). Where such areas abound, gravid females presumably do not need to make extensive movements in order to nest. But in densely forested habitats where suitable clearings are scarce, iguanas gather together in large numbers to nest at the available sites, some presumably having

migrated considerable distances to do so (Rand 1968).

Nesting movements such as these are exceptional in lizards. Typically female lizards nest either within their home ranges or at most make only limited excursions from their home ranges to the site of nesting (i.e., Blair 1960, Parker and Pianka 1976). Besides green iguanas, the only other well-documented cases of extensive (> 1 km) nesting migrations in lizards are in two closely related genera: *Conolophus* (Werner 1982, Christian and Tracy 1982) on the Galapagos Islands and *Cyclura* (Wiewandt 1977, 1982) in the West Indies. As in the green iguana, their movements appear to be in response to a scarcity of soils on these islands that are suitable for nesting.

We report here the results of our investigation on the nesting migrations of green iguanas (*Iguana iguana*) which inhabit the dense semi-deciduous lowland forests of Barro Colorado Island (BCI) in Gatun Lake of the Panama Canal. Each year in mid-dry-season, gravid females congregate to nest in several open clearings located on small islands around BCI. We have carried out an intensive mark-recapture effort over four successive nesting seasons to investigate nesting site fidelity in these lizards. We were also able to monitor the movements of a number of iguanas away from one nesting site using radio-telemetry techniques.

METHODS

The most accessible and consequently most thoroughly studied BCI nesting site is located on the 0.3 ha islet of Slothia which lies adjacent to the laboratory clearing on BCI. Previous studies of iguana nesting there have relied on unobtrusive observation, but in 1979 we captured several gravid females on Slothia by noosing them from a blind located at the edge of the nesting clearing. After their release, the iguanas returned to the clearing and continued nesting. During the 1980 nesting season we intensified our noosing efforts and still found no evidence that we were significantly disrupting nesting on Slothia. Most captured iguanas were seen back in the clearing shortly after their release, and those present in the clearing during a noosing attempt soon returned to their activities. We therefore noosed iguanas intensively during the 1981, 1982 and 1983 nesting seasons as well.

In 1981, construction activity at a site on BCI about 200 m away from Slothia produced a clearing that attracted nesting iguanas. We placed live-animal traps covered with palm fronds for shading around this new area and found that the iguanas readily entered the traps while exploring this new nesting site. This Construction Clearing site was trapped again in the same fashion during the 1982 and 1983 nesting seasons.

In 1981 and 1982, iguanas were also trapped and occasionally hand-captured from within their burrows at other known nesting sites around BCI (Fig 1). In 1983, the dry season began early and was unusually severe, producing exceptionally low lake levels. We therefore shifted our trapping emphasis in 1983 to the numerous beaches that had formed along the BCI shoreline. We were interested in how the iguanas would respond to these natural potential nesting areas that had not been

available to them during the previous years.

Captured iguanas were weighed, measured, marked, and released at the site of capture to finish laying. Marking involved systematically clipping the dorsal crest scales so as to give each iguana a unique, individually characteristic pattern of missing scales. No evidence of regeneration of scales was observed over the course of this study.

The details of our investigation of iguana movements as determined through the use of radio-telemetry will be presented elsewhere (in preparation). Here we merely report the information obtained relating to those iguanas successfully tracked as they moved away from Slothia during the 1979, 1982 and 1983 nesting seasons. Radio-transmitters were force-fed to five iguanas in 1979 and four iguanas in 1982. In 1983, the transmitters were mounted upon acrylic saddles and glued to the lower backs of four iguanas.

RESULTS

A majority of the iguanas that visited the Slothia nesting site during the 1981, 1982 and 1983 nesting seasons were captured; all but two of the iguanas that nested on Slothia over this period were marked individuals. A total of 142 different iguanas were seen on Slothia during one or more of the four nesting seasons in which iguanas were intensively noosed. Of the iguanas seen on Slothia in a given nesting season, between 30−45% returned again the next year, and those iguanas seen over two consecutive nesting seasons had an even higher probability (44−55%) of returning. Of the 15 iguanas whose first and last captures spanned three years, 13 were seen in all three years and two missed the intervening year. Of the eight iguanas whose first and last captures spanned four years, five were seen in each year, and the remaining three skipped only one year.

All of the iguanas seen on Slothia during this study had been marked there originally, except for two iguanas that had been captured previously in traps at the nearby Construction Clearing site. A total of 23 iguanas were trapped in the Construction Clearing site from 1981 to 1983. Seven iguanas were captured either at this site or on Slothia in one year and on the other site in a subsequent year, and six iguanas were seen on both sites during the same year. Given the close proximity of these two sites and the evidence of free movement between them, they will be considered hereafter as a single, collective nesting aggregation. The traps at the other nesting sites and beaches around BCI yielded an additional 144 marked iguanas from 1981 to 1983. Most of these iguanas were captured at the nesting aggregations of DeLesseps and Mosca. Our impression is that we captured only a small fraction of the iguanas that visited these sites each year. There was also limited nesting activity on the small island of Pepper in 1981 and 1982, but none during 1983. In 1983, tail tracks in the sand revealed that iguanas were exploring most of the newly formed beaches, and there was actual nesting on two of these: a mainland beach that suffered heavy clutch predation and an insular beach that experienced a successful hatch (see Rand and Robinson 1969, Drummond 1983).

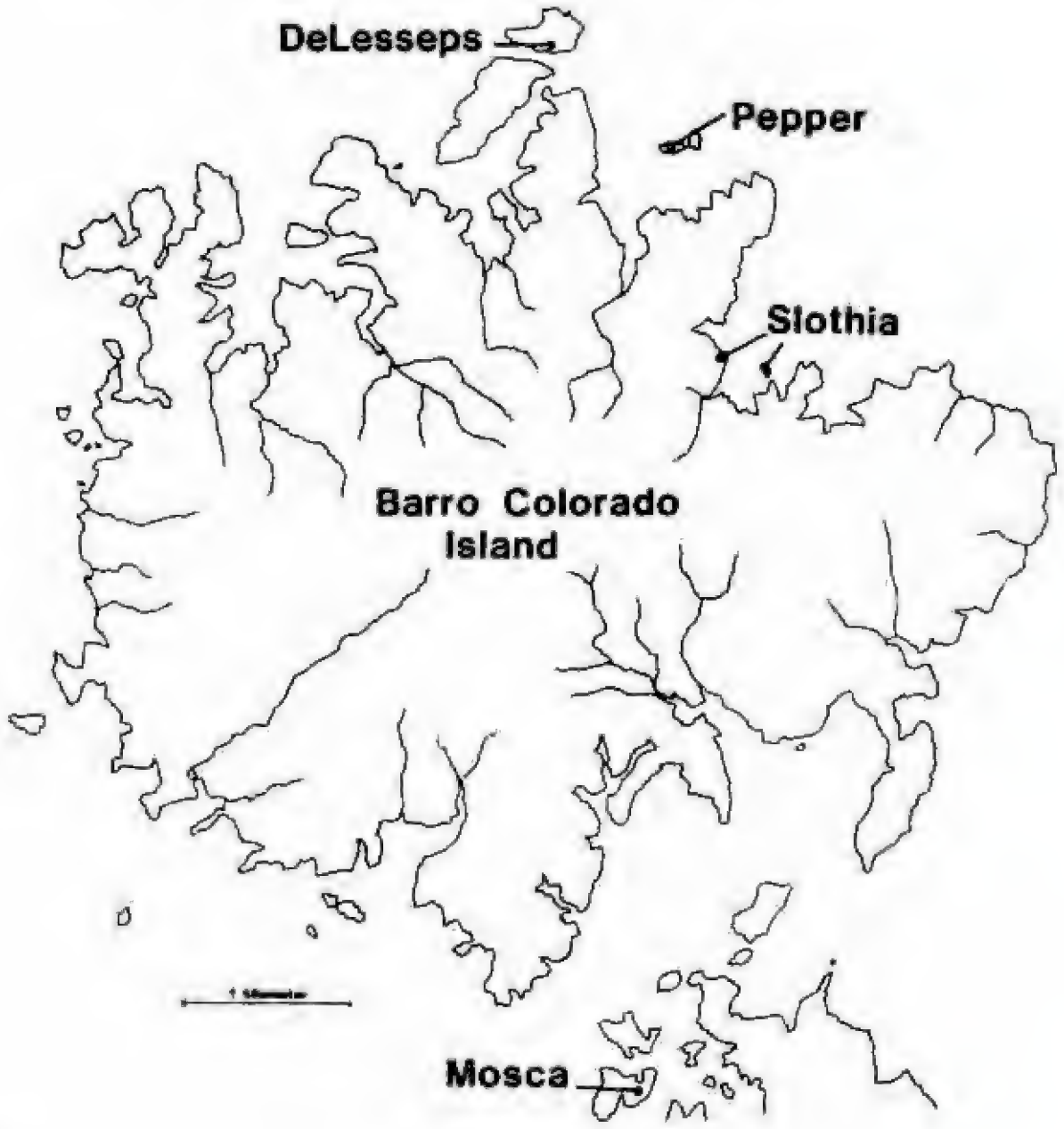

Figure 1
Locations of iguana nesting sites around Barro Colorado Island, Lake Gatun, Panama.

During the four years of intensive capturing, 307 individual iguanas were marked at the various nesting sites around BCI. Fifty-five iguanas were recaptured at least once at these sites over successive nesting seasons (Fig 2).

Radio-telemetry efforts produced information on the movements away from Slothia of five iguanas in 1979 and of four iguanas in 1982. Four iguanas were radiotracked away from Slothia in 1983; of these, two were individuals that had also been successfully followed in 1982 (Fig 3). After leaving Slothia the iguanas occasionally remained on the adjacent BCI shoreline for a few days but would then move fairly rapidly and directly for short to moderate distances (< 1.5 km). Movements stopped as abruptly as they began, and the iguanas made only minor local movements thereafter until their transmitters were lost. All movements were confined to areas of BCI near the lake's shoreline.

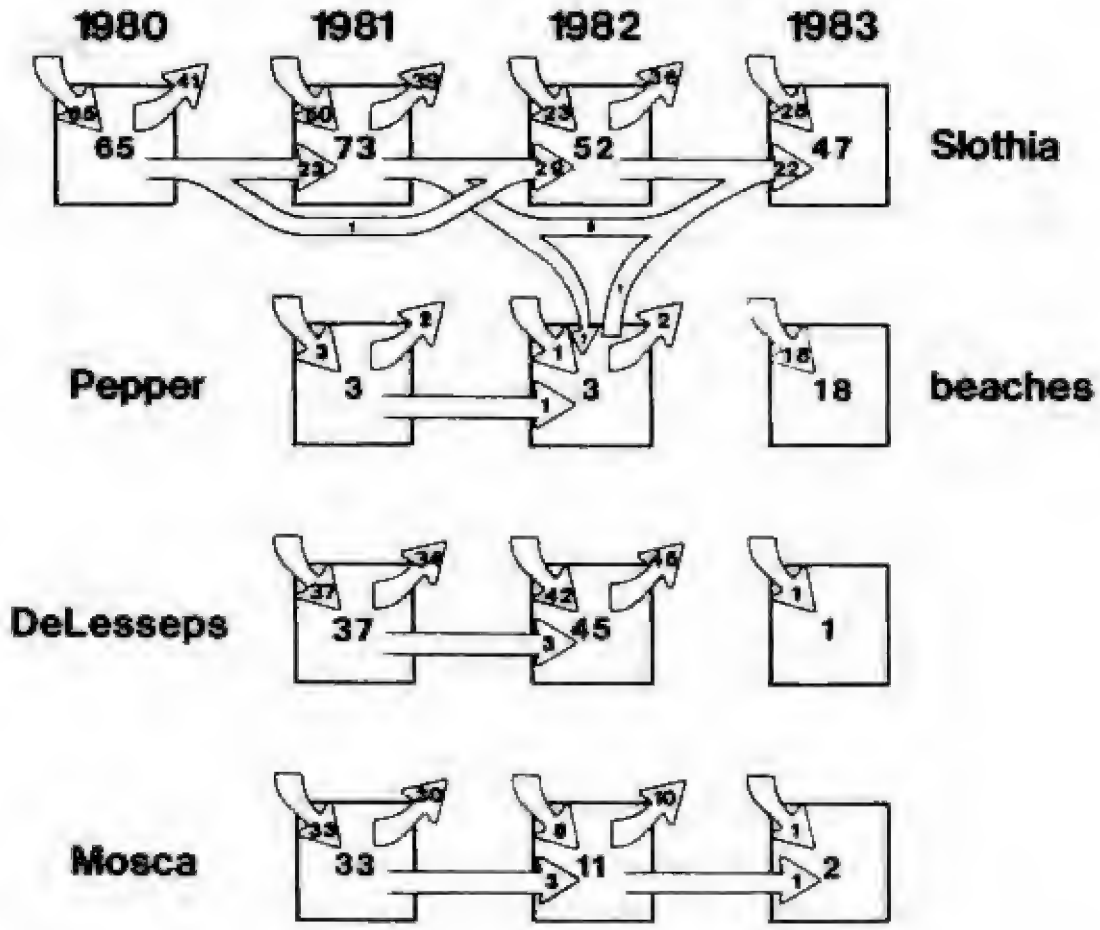

Figure 2

Recapture results for nesting iguanas over four nesting seasons. Arrows into cells indicate the number of new iguanas marked at a site that year; arrows out of cells indicate the numbers of iguanas that were captured at a site and not seen again, and arrows between cells represent recaptures over years.

DISCUSSION

While iguanas obviously do explore and occasionally nest in new areas that become available to them, our evidence seems to indicate strong fidelity once they locate a suitable nesting site. Our results may even underestimate the actual amount of nesting site fidelity: some of the iguanas marked at DeLesseps and Mosca in 1981 probably returned in 1982 but avoided the traps. This seems especially likely given that only three of the 161 trapped iguanas released during this study were re-trapped again during the same nesting season, despite the fact that we repeatedly saw marked iguanas fleeing the nesting area as we approached to check the traps. This learned avoidance of the traps probably contributed to the low recapture rates at the trapped sites over successive nesting seasons as well.

Although noosing and trapping disturbances could have caused the iguanas to change nesting sites during the years of this study, only one instance of cross-over between nesting sites was documented (Fig 2). An iguana captured on Slothia in 1980, 1981 and 1983 was trapped in 1982 attempting to nest at the clearing on the island of Pepper, located approximately midway between the Slothia and DeLesseps nesting sites. If substantial numbers of other iguanas changed nesting sites from year to year, we would have expected more of the trap-naive Slothia iguanas to have been trapped while nesting elsewhere and certainly should have noosed any DeLesseps or Mosca iguanas had they appeared on Slothia.

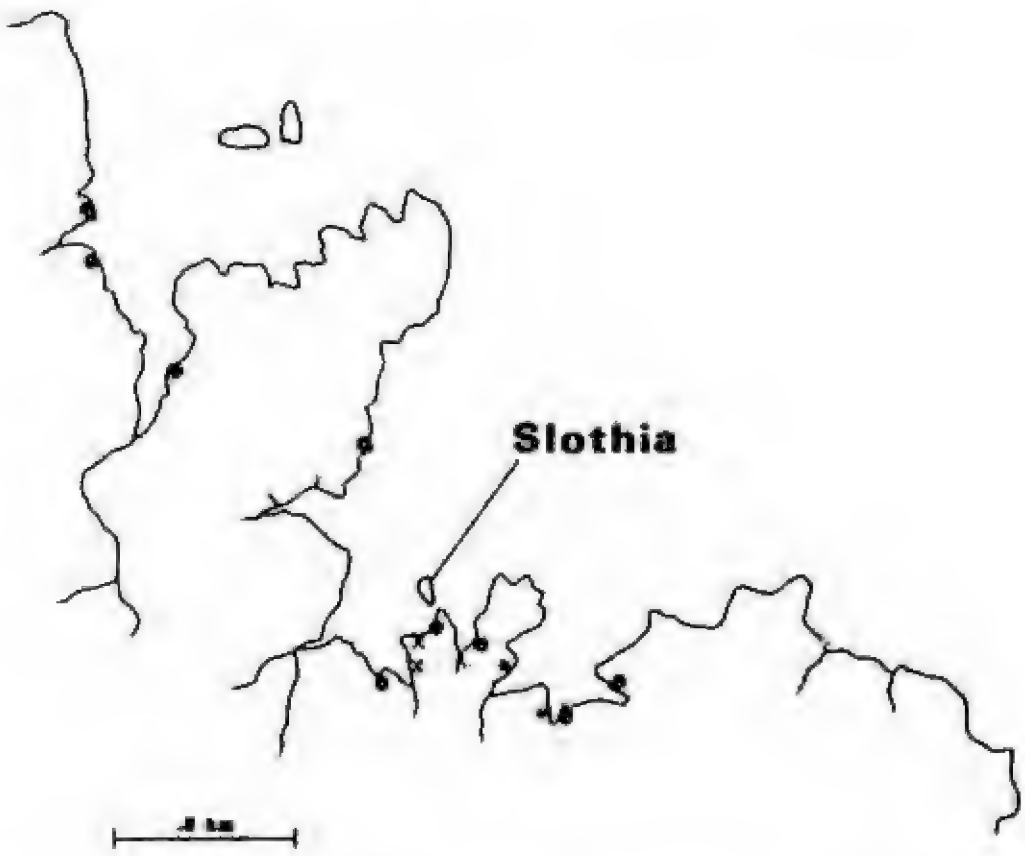

Figure 3

Points of return for iguanas that were followed away from the Slothia nesting site, as determined by radio-location. The × and * characters represent two different iguanas that were successfully followed over two consecutive nesting seasons.

When many of the iguanas marked in 1980 were not seen again the following year, we initially suspected that the iguanas might be skipping years reproductively. Since clutch size and female size are highly correlated in iguanas (Fitch and Henderson 1977, Rand 1984), we thought that some iguanas might be foregoing reproduction in a given year to invest more energy towards growth, so that larger clutches could be produced in subsequent nesting seasons. Of the 55 iguanas recaptured during this study, however, only six were recaptured over nonconsecutive years, and each of these iguanas may well have nested undetected at the Construction Clearing site during their year of absence. Also, five of these six iguanas were larger than average when first captured, and none experienced marked growth over the year they were not seen. Thus female iguanas appear to nest every year after they reach sexual maturity. The fate of the numerous iguanas marked each year and not seen again still remains unexplained. Rates of return over successive years on Slothia varied from 30–45%, and an additional 10% or so of the iguanas not seen in a given year were known to be elsewhere. Thus between 45–60% of the iguanas marked each year were never seen again. Adult iguanas do experience predation (Greene, Burghardt, Dugan and Rand 1978); ten of the 55 iguanas we recaptured showed evidence of tail loss between the year when they were marked and their next capture. But unfortunately our knowledge of iguana demographics is insufficient at present to enable us to say whether adult mortality rates of this magnitude are reasonable. We suspect that mortality only accounted for a portion of the marked iguanas that were not seen again.

Another unresolved question, probably related to the disappearance of the marked iguanas, is why so many of the iguanas seen on Slothia each year were not seen to nest there. We have no evidence that they were going to any of the other known nesting sites around BCI, but the possibility exists that there may have been scattered isolated nesting which we did not detect. If so, the iguanas certainly were using areas that we would consider at present to be unsuitable for incubation purposes.

Three gravid iguanas were successfully radiotracked away from Slothia but provided no clues as to where else iguanas might be nesting. But both gravid and spent iguanas moved only moderate distances from Slothia (Fig 3), and except for brief crossings of peninsulas, no inland movements were observed. The two iguanas that were followed over successive years each returned to the same general vicinities each year, suggesting returns to established home areas. The limited movements of these iguanas away from Slothia and the strong nesting site fidelity shown by those that returned to nest over successive years are consistent with the possibility that the iguanas are philopatric to their natal site. During the years preceding this study, more than 700 hatchling iguanas were toe-clipped and released near Slothia. We recaptured seven of these as nesting females, all on Slothia.

Hatchling iguanas are known to go through a brief dispersal phase but soon settle down (Drummond and Burghardt 1982), and iguanas appear to remain quite sedentary thereafter, both as juveniles (Henderson 1974) and as adults (Dugan 1980). Limited hatchling dispersal followed by sedentariness might be advantageous to these iguanas if the scarcity of suitable nesting sites around BCI is limiting to them. Females remaining near their natal site would stand a better chance of re-locating this proven site when they first nest, and would also minimize the costs of their nesting migrations. If males also remain near their natal site in order to insure access to such females, then the iguana population around BCI could be clumped into semi-isolated demes associated with each nesting site. Electrophoretic data to be presented elsewhere (Bock and McCracken, in preparation) suggest that there is indeed a restriction of gene flow between Mosca, the most isolated nesting aggregation, and the other two major nesting sites of Slothia and DeLesseps.

ACKNOWLEDGMENTS

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LONG RANGE MOVEMENTS OF LARGE TERRESTRIAL MAMMALS

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ABSTRACT

Many species of large mammals perform long range movements, some of which are annual migrations, to occupy environments that are only seasonally favorable. Movements may be altitudinal in mountainous areas, latitudinal in northern areas, or from dry to wet regions in dry tropical areas. They may vary from movements between highly specific home areas that are passed on by tradition from parent to offspring (as in deer and bighorn sheep), to broad regional population shifts between suitable seasonal ranges (in species such as caribou and wildebeest), to true nomadism (species such as bison and saiga antelope). The latter species form large social groups and occupy large expanses of homogenous environments. Dispersal is related to social structure, population genetics and population dynamics. In expanding populations, dispersal can result in rapid range extension as shown by rate of spread of large mammals introduced into unoccupied habitat. Highly gregarious species disperse by budding off of social groups, while more solitary species disperse as individuals. Dispersal is induced by social interactions between parent and offspring and between social competitors. In nomadic species, movements by large aggregations accomplish the functional role of dispersal. Dispersal has implications for gene flow and inbreeding/outbreeding coefficients as well as distribution of populations over available habitats of differing quality and quantity.

INTRODUCTION

Movements of large mammals, which in this paper are taken to include ungulates and carnivores of approximately 40 kg or greater in weight, can be categorized roughly into local movements, migration, dispersal and nomadism (Lidicker and Caldwell 1982, Shields 1982). Local movements are those encompassed by daily travels to obtain food, water, escape or concealment cover, den sites, etc., plus minor seasonal shifts as resource availability changes. Because many large mammals have high mobility, the range of local movements can be large. This review will focus on movements that exceed local movement patterns.

Migration can be defined as more or less consistent seasonal shifts of the population between different geographic areas in response to seasonal changes in resource availability and quality. At their most extreme, migrations may take animals from a geographic area that is totally uninhabitable at some season. In less extreme cases, migrations are related to high seasonal amplitude in resource quality, such as movement from an area of dry vegetation to one with green growing vegetation for a herbivore species.

Dispersal is a movement from one geographic area to another that is not related to seasonal resource availability. It typically results in non-return and is a more permanent change in distribution of individuals or social groups than is migration.

Nomadism is broad-scale movement that is erratic or random in space, but not necessarily in time.

Movements of large mammals form a rich array of shifts in location in response to a complex set of environmental and social variables. The boundaries between local movement, migration and dispersal are blurred, and the categories are arbitrary. Thus the categories are a matter of convenience and may be taken as "archetypical" models influenced by habitat characteristics and climate.

MIGRATION

Altitudinal migration

Altitudinal migration is well represented by mule deer (***Odocoileus hemionus***) and elk (***Cervus elaphus***) in the mountainous regions of the western United States. Migrations result in annual movement from high altitude summer ranges that cannot be occupied during time of deep snow depths, to milder winter range at lower elevations. Leopold, Riney, McCain and Tevis (1951) describe migratory movements of mule deer in the Sierra Nevada of California as movements along a migratory pathway between individual home ranges on the summer areas in the mountains and individual home ranges on the wintering areas in the western slope foothills. Fidelity to given home ranges has been confirmed by subsequent studies with marked and radio-collared animals. Leopold et al. (1951) assumed that each major watershed was a self-contained unit of deer range, and the simplest movement pattern for migration would be perpendicular to the mountain slope, without lateral movement. However, subsequent studies of marked deer showed that they did not follow the simplest pattern. For example, Gruell and Papez (1963) trapped and marked 789 mule deer over 4 years on 12 winter ranges in northeastern Nevada. In performing seasonal migrations, deer on given winter ranges did not simply migrate to the nearest or even nearby summer ranges but scattered broadly to widely separated summer ranges. The male with the longest movement covered 155 airline km, crossing 6 mountain ranges to summer in Idaho (Gruell 1958). The female with the longest movement covered 130 km over 7 mountain ranges. These movements are remarkable, given that once on the home range at either end of the migration, individual deer remained within

several km. Neither did animals on a given summer range move to a specific winter range. In some cases the movements of individual deer crossed as each moved in the opposite direction between summer and winter ranges. In the reverse experiment, Ashcroft (1961) marked 115 deer over 2 years on summer range in the western Sierra Nevada in California. These deer migrated to 7 different winter ranges, only 2 of which were down drainage.

Clearly migration by mule deer is not the result of moving the shortest distance in elevational gradient that would take the individual from a suitable summer area to a suitable winter area. The unpredictability of individual movements can be understood on the basis of the origin of such movement patterns in the social structure of the population. First, learning of home ranges and the migratory pathway occurs during the first year that the offspring is with the mother, and this tradition is continued via mother-offspring association. Second, deer have well-developed dispersal patterns based upon individual movement of offspring from the mother's home area. Males typically disperse widely and such patterns are established during the first year. Females often settle near the mother but sometimes disperse over greater distances, and dispersal patterns are usually established later, at 2 or 3 years of age. Direction of dispersal appears to be random, except to the extent that preferred habitat is nonrandomly distributed. Given that individual migration is the accumulation of generations of learned migration routes and home ranges, elaborated by dispersal at each generation, it is easy to see why erratic patterns have developed.

Origins of new migratory patterns have been observed that reinforce the role of tradition in the development of such patterns. Prior to about 1950, the upper reaches of the McKenzie River drainage in the western slope of the Cascade Mountains in Oregon were covered by a vast old-growth forest of 400- to 600-year-old Douglas fir (*Pseudotsuga menziesii*), a vegetation type supporting virtually no deer. Deer occurred mainly on river flood plains along the McKenzie River where flooding and meandering of the river channel created favorable habitat. A few deer apparently migrated to summer ranges around mountain meadows in the headwaters where open areas occurred naturally. Beginning in the 1950's these old-growth forests began to be opened up by logging in a patchwork of block clear-cuts. Deer, presumably offspring of deer already migrating to natural meadows, quickly occupied the new, favorable habitat patches. The first deer were usually observed the year following clear-cutting, as vegetation resprouted, and these deer were typically yearlings. Fall migration occurred prior to the breeding season, and deer from the higher mountains moved down to the McKenzie River Valley, where they intermingled with deer that were resident year-round in the valley (McCullough 1964). Thus populations that were resident were interbreeding with long-range migrants from natural meadows and shorter range migrants occupying newly logged areas, as well as with subpopulations which shared a common gene pool that had migrated into alternate secondary drainages. However, in the following spring, individuals from these various subunits of the population resegregated over the available summer habitat according to their learned movement patterns.

Reginald Barrett (University of California, Berkeley) has brought another case to my attention. On Dye Creek Ranch, a deer wintering area on the northern edge of the Sacramento Valley in California, there was no resident, nonmigratory population. A ranch worker captured fawns on the summer range and hand-reared them on the ranch, and this nucleus has expanded into a resident, nonmigratory population.

While intermingling of interbreeding populations is common on winter ranges, some non-interbreeding populations intermingle on the summer range. Thus the black-tailed deer (*O. hemionus columbianus*), a well-marked subspecific form of mule deer, commonly overlaps with the typical Rocky Mountain mule deer (*O. h. hemionus*) on the summer range in high mountains of Washington, Oregon and California, and the forms are sufficiently distinct as to be readily recognized in the field. There is hybridization along the crest of the Northern Cascades (Nellis, Fairbanks, Terry and Taber 1974), but further south, winter storms prior to the breeding season push black-tailed deer west of the divide and Rocky Mountain mule deer east, to separate winter ranges, and the forms remain distinct. In certain places in Oregon, some black-tailed deer move east, and hybrid swarms occur.

Factors that trigger migratory movements are subtle despite the obvious role of the ultimate factor, winter snow depth. Deer cannot move effectively in snow depths greater than about 46 cm (Loveless 1967; Gilbert, Wallmo and Gill 1970). Spring migrations are not controlled by the snowline (Russell 1932, Leopold et al. 1951, McCullough 1964). Russell (1932) and Leopold et al. (1951) thought that spring migrations were controlled by the appearance of new, green plant growth at the higher elevations. Track counts made by deer as they crossed a dirt road during spring migration showed that females and yearlings started to migrate earlier in the season than bucks. Numbers of migrating deer increased slowly at first, then rose rapidly to a peak, after which they descended sharply. During the migration, a drop in temperature, especially if accompanied by stormy weather, resulted in a slowing down of the migration (Wright and Swift 1942).

Russell (1932), Leopold et al. (1951), and Leach (1956) reported that fall migrations of deer are initiated by fall storms that drive the deer from higher elevations. In some cases, however, fall migrations cannot be explained on the basis of snow storms. Russell (1932) reported that in Yosemite National Park (California) the fall migration may precede snowfall by as much as two months and is related to temperature change. Fischer, Davis, Iverson and Cronemiller (1944) reported that according to local folklore, fall migrations of the Interstate deer herd (Oregon–California) start with fall storms, when actually they start with an almost imperceptible change in weather. Rasmussen (1941) reported that the Kaibab (Arizona) deer herd very definitely shows responses in their migration activities that cannot be explained on the basis of climatic changes, available food, lack of water, snow depth or unfavorable terrain. In a study of migration of Oregon deer, McCullough (1964) found that both the spring and fall migrations were closely correlated with changes in relative humidity. Furthermore, a summer reverse migration apparently occurred due to aseasonal changes in relative humidity.

Given the complex migratory pathways, it would be unlikely that the movements of all individuals would be synchronous or in response to the same stimulus. Deer having to cross several mountain ranges can hardly wait for fall snow storms to drive them out of the summer range since the same snow storms may block their paths. Deer that must cross high divides to reach the slope on which they winter must precede storms that produce deep snow. In a good food year, deer that summered on the west slope but wintered on the east slope of the Sierra Nevada in California arrived in the winter range in November; in the following year, a poor food year, deer numbers on the core winter range remained low until February despite heavy snowfall at high elevations (McCullough 1969). In another case, radio-collared elk on the western slope of the Cascade Mountains in Washington did not leave the summer range in a cold but snow-free winter until late snowfall occurred (R. D. Taber, personal communication).

Other North American species that show altitudinal migration are elk (***Cervus elaphus***) and bighorn sheep (***Ovis canadensis***). Both of these species differ from deer in social structure, ordinarily living in medium to large social groups, while deer are solitary or form small groups. Migration in elk has been reviewed recently by Adams (1982). In general pattern it is similar to that in deer, with resident and migratory herds intermingling in winter areas (Martinka 1969, Houston 1982). Winter grounds in this species tend to be open grassy valleys and foothills while summer range is in more timbered areas in the mountains. Studies of individual associations between marked animals showed little consistency of social groupings, with individuals switching groups frequently (Knight 1970). However, most studies show a larger herd unit consistency (McCullough 1969), and this conclusion agrees with observations that most individuals summer and winter in the same areas from year to year, with a certain degree of dispersion due to dispersal (Picton 1968; Knight 1970; Craighead, Atwell and O'Gara 1972).

Bighorn sheep show migratory movements between highly specific summer and winter areas. While elk and deer show relatively broad habitat requirements and tend to be rather broadly distributed, bighorn sheep have isolated ranges because of their dependence on steep rocky terrain for escape cover (Smith 1954, McCullough and Schneegas 1966, Geist 1971, Wehausen 1980). Because suitable summer and winter habitat is patchily distributed, the maintenance of traditions in the population is important (Geist 1971). If the only individuals familiar with the location of a given habitat patch are lost to the population, the traditional transmission of knowledge will be lost, and the use of that area discontinued. Because bighorn sheep are conservative dispersers, rediscovery of a suitable habitat patch through natural range expansion is a slow and uncertain process.

Geist (1975) has advocated that restoration programs through reintroduction be based on hand-rearing of lambs, with humans leading the naive young animals from winter range to summer along appropriate migration routes. Subsequently, yearling wild animals can be integrated into the group of experienced yearling animals that know the suitable areas and migratory pathways. Bergerud (1974) used calves to reestablish woodland caribou (***Rangifer tarandus***) into Newfoundland in order to

prevent dispersal from the release site.

The problem of isolated habitat patches for bighorn sheep in a vast area reaches extremes in the Sierra Nevada Mountains in California (Jones 1950, McCullough and Schneegas 1966, Wehausen 1980). A few steep rocky canyons on the eastern scarp are the only suitable winter ranges, and suitable summer areas are highly localized along the crest. Migratory paths are associated with an extreme scarp in which about 3,000 m elevational change occurs over a lateral distance of about 5,000 m. Attempts to reestablish populations of the Sierra sheep have been based on relocating animals to appropriate wintering areas in winter and allowing them to migrate upslope to summering areas on their own. Nine released animals remained on those winter ranges and migrated to summering areas (Andaloro and Ramey 1981). However, in the following winter most of the animals remained at high elevation (about 3,000 m) despite large snowstorms. Only an ewe and her lamb returned to the winter range. Animals wintering at high elevation suffered high mortality (5 animals). Similar failure of relocated bighorns to migrate to lower elevation was reported in Colorado (Bear 1979). In April the survivors returned to low elevation and eventually joined the ewe and lamb that wintered at low elevation. In 1980, 10 additional sheep were introduced, and in the following winter 20 bighorns were observed on the winter range. The relocated animals have established winter and summer ranges with migratory routes connecting them and by all indications are now a successful population (Andaloro and Ramey 1981). A more complete review of problems related to conservation of large mammals by reintroduction to original ranges from which they were extirpated is given by Jungius (1978).

Lateral Migration

Many species of ungulates migrate from unfavorable to favorable areas seasonally by lateral movements. White-tailed deer in the eastern United States near the northern boundary of their range showed this behavior (Severinghaus and Cheatum 1956, Siglin 1965). These migrations may be made in any direction and take deer from good summering areas to good wintering areas, usually referred to as "deer yards" because of the high density of animals. Yards are extensive stands of conifers, most commonly white cedar (*Thuja occidentalis*), that grow with closed canopies in lowlands. The green canopy forms an infrared thermal shield to reduce radiant heat loss, and because the canopy collects snow, evaporation and melting lower snow depth under the canopy (Ozoga 1968). The high density of deer results in a packed trail system in the snow that facilitates movement, and white cedar is a good food species. Furthermore, basic metabolic rate of deer is reduced in winter (Silver, Colovos, Holter and Hayes 1969; Seal, Verme, Ozoga and Erickson 1972), and food intake is voluntarily reduced (Ozoga and Verme 1970).

Individual deer show fidelity to given summering and wintering areas (Verme 1973, Nelson and Mech 1981). Adult deer livetrapped in one yard and released in nearby yards returned to their "home yards" and were recaptured in the same or following winter (Switzenberg, as cited by Verme 1973). Some returned within a

week despite deep snow. However, only 2 of 78 relocated fawns were recaptured. It is not known if they did not attempt to return or suffered high mortality in the attempt.

Lateral movements of white-tailed deer between summer and winter areas show the same criss-cross pattern as previously described for altitudinal movements of mule deer (Verme 1973, Nelson and Mech 1981). Thus discrete population "units" are not represented in migrations; rather migration is undertaken by individuals or small social groups, each following its own pathway between a given summering and wintering area. Once again tradition passed from mother to young, as modified over time by dispersal, seems to be the basis of this pattern.

While snowfall and its impediments to deer locomotion may be the ultimate factor favoring migration, temperature changes were reported to be the proximal factor triggering migration (Verme 1973, Nelson and Mech 1981). Sometimes changes in temperature caused reversal of migration, such that animals that had moved to the winter range returned to the summer range (Nelson and Mech 1981), similar to the reversal reported by McCullough (1964) for humidity changes in black-tailed deer. Once again it seems likely that appropriate proximal factors that trigger migration are also learned, since the distances, directions, intervening barriers, etc., vary with the individual migratory pattern.

Lateral migrations reach their greatest extent in species of ungulates that occupy large open areas of grassland or tundra. These species form large aggregations that, in the absence of escape cover, are necessary as anti-predator strategies (McCullough 1969, Hamilton 1971, Bergerud 1974b, Estes 1974, Kitchen 1974, Hirth and McCullough 1977, Sinclair 1977). Because the herd serves different functions according to habitat type and because the herd is mobile, these species are freed from dependence on known home areas, and philopatry is poorly developed. Furthermore, the food of these animals tends to be of very low quality over much of the year and distributed widely over relatively homogeneous environments of immense scale. These factors favor much more erratic movements that verge on being truly nomadic in some cases. Distribution varies unpredictably within a year and between years.

In northern regions, caribou and reindeer perform extensive seasonal movements that tend to be north-south in orientation due to the extremes in climate (see Bergerud 1974b, Kelsall 1968). Generally, caribou spend the summer in open tundra in the far north and migrate to taiga, the timbered areas to the south, for winter. Banfield (1954) reported midsummer southward movements from the extreme north; this movement culminated in early summer and was followed by a return in late summer to more northerly areas. In fall, snow storms prompt movements back to the taiga for winter. Thus there is a major migratory movement in spring and fall, with a minor migration in the reverse direction in summer. Some traditional routes of movement are usually followed but may be abandoned in given years (Kelsall 1968), with dire results for native peoples dependent upon caribou for food. The same general pattern appears to hold for domestic reindeer in the old world. Woodland caribou, a subspecific form occupying the more southerly boreal forest in North America, are largely nonmigratory or, in the more northern areas, show relatively short movements

between summer and winter range (Simkin 1965).

In African savannas and plains that are near the equator, dry seasons rather than winters become the major force favoring migratory behavior in large mammals. Although many species show spatial shifts between the wet and dry seasons, the most pronounced migrations are performed by wildebeest (***Connochaetes taurinus***), zebra (***Equus burchelli***) and Thomson's gazelle (***Gazella thomsonii***) (Schaller 1972, Kruuk 1972, Sinclair 1977, Maddock 1979). Wildebeest, the species showing the most spectacular migrations, form large aggregations and migrate in search of green grasses. They move from the southeastern plains in the dry season to the woodland savannas in the northwest where moister conditions prevail. Movements of zebra and Thomson's gazelle are similar but less elaborate and involve much smaller aggregations. There is a clear grazing succession with zebra being first and taking the coarsest grasses, followed in several weeks by the more selective wildebeest, which in turn is followed by the most selective Thomson's gazelle (Gwynne and Bell 1968, Bell 1971, McNaughton 1976).

There are many irregularities in movements due to distribution of rainfall (Pennycuick 1975), occurrence of fire (Anderson and Talbot 1965), previous grazing, and life history requirements for birth and breeding (Maddock 1979). However, populations of these species that live in more favorable and stable environments are nonmigratory. In Ngorongoro Crater, for example, these species become sedentary and occupy home areas or move only small distances (Estes 1969, Klingel 1967, Kruuk 1972).

NOMADISM

In temperate areas, bison (***Bison bison***) in the New World and saiga antelope (***Saiga tatarica***) in the Old World show nomadic, broad-scale movements. Roe (1970) reviewed the early records of accounts of bison on the prairies and great plains of North America. He concluded (pp. 594–595) that there was no convincing evidence for regularity in movements of bison; on the contrary, bison movements showed "an imponderable, incalculable, wholly erratic and unpredictable caprice." It must be recalled that this region is characterized by low topographic relief, relatively low snowfall, and homogeneous vegetation in the uplands that constitute most of the area. Also, bison are large, winter-hardy animals. In the mountainous areas of Yellowstone National Park, bison show regular migratory movements between traditional summering and wintering areas (Meagher 1973). Considerable exchange between subpopulations occurs even in winter with deep snows.

The saiga antelope is a small antelope (males 43 kg, females 31 kg) that occupies steppe grasslands of the Soviet Union where it occurs in great abundance and forms large herds (Bannikov, Zhirnov, Lebedeva and Fandeev 1967). It is nomadic, much as the bison in North America, with movements changing with season, climate and between years, as the animals seek out suitable pasturage and avoid winter extremes.

MOVEMENT OF CARNIVORES

Large carnivores exist at much lower density than their prey, and their winter ranges are often extensive. Wolf (*Canis lupus*) packs in northeastern Minnesota have ranges between 110 and 2580 km^2 (Mech, Frenzel, Ream and Winship 1971) and on Isle Royale 270 to 545 km^2 (Mech 1966). Home ranges from other areas reviewed by Mech (1966) range from 90 to 1400 km^2. Clearly the "home" areas of some carnivores exceed the distances covered by a number of "migratory" ungulates discussed above. Home range sizes of 23 grizzly bears (*Ursus horribilis*) radio tracked in Yellowstone National Park ranged from 190 to 1640 km^2 (Knight, Blanchard and Kendall 1982). Home ranges for mountain lions (*Felis concolor*) (see review of Anderson 1983) in Idaho ranged from 140 to 290 km^2 (Seidensticker, Hornocker, Wiles and Messick 1973), 120 to 160 km^2 in Arizona (Shaw 1979), and 230 to 1825 km^2 in Texas (McBride 1976). In west Texas, mountain lions moved between mountain ranges that were separated by desert areas of low prey density. Similar large home ranges or territories are typical of large carnivores in Africa (Schaller 1972; Kruuk 1972; Frame, Malcolm, Frame and van Lawick 1979).

Carnivores are forced to respond to movements of their prey base. Bears, which are marginal predators on large ungulates and take mainly the very young or the sick and injured, go into deep sleep (not true hibernation) over winter in extreme environments. Thus, they do not need to follow movements of prey. Mountain lions follow altitudinal migrations of their prey, and tundra wolves follow the movements of their major prey, caribou. Wolves in the northeastern United States do not migrate, but rather maintain large home ranges that encompass summer and winter ranges of white-tailed deer. Mech (1977) and Nelson and Mech (1981b) present evidence that deer select disproportionately for areas that lie on the boundaries between wolf packs and thus are subject to lower predation pressure because each pack avoids the boundary where aggressive encounters between packs are likely.

In the east African savanna and plains, lions do not follow the migrations of wildebeest, zebra and Thomson's gazelles but remain in pride territories (Schaller 1972). Spotted hyenas (*Crocuta crocuta*) migrate to some extent but do not follow the full movement of wildebeest (Kruuk 1972). Wild dogs (*Lycaon pictus*) also remain on permanent territories (Frame et al. 1979). The inability of these large predators to follow migrations has been attributed to the needs of non-mobile young. Kruuk (1972) found that hyenas in Ngorongoro Crater formed clan territories, were nonmigratory, and lived at population densities much higher than their more mobile conspecifics on the Serengeti.

DISPERSAL

Dispersal capability in large mammals is substantial, as shown by rate of spread of species introduced into new environments. Caughley (1963) reported rates of spread of 9 ungulates introduced into New Zealand, where ungulates were not endemic. These ranged from 8.7 km^2 per yr for chamois (***Rubricapra rubicapra***) to 0.6 for elk.

Among ungulates, three major patterns of dispersal are observed that are related to their social systems.

Dispersal in Solitary Species

Species with solitary or small group formation, most of which use cryptic strategies to avoid predation, disperse as individuals. This system is best suited to colonization of new habitats, and it is probably not accidental that many of these species occupy subclimax vegetation types that occur irregularly in time and space. Food quality varies greatly due to rate of plant growth, and plant growth is highest where recent disturbance of a tree canopy allows sunlight to reach ground level and where competition for water and soil nutrients is reduced.

Male white-tailed deer disperse as yearlings; they are driven away by their mothers as time of birth of new fawns approaches. It is not surprising that yearling males are the first animals to be observed in newly created patches of subclimax vegetation. Dispersal of white-tailed deer usually leads to emigration from favorable habitat to poor habitat (Hawkins and Klimstra 1970, Kammermeyer and Marchinton 1976) and from high to low density (McCullough 1979). However, net dispersal is related to economic density (related to carrying capacity) rather than density per se. Robinette (1966) showed that mule deer dispersed from lower to higher density areas if relative availability of resources was greater in the area of higher absolute density. Dispersing yearling males are subjected to high mortality rates (McCullough 1979).

Dispersal of females in white-tailed deer shows a distinctly different pattern. Although yearling females are excluded by their mothers at the same time as males, they remain in the vicinity and later are allowed to rejoin the mother when the new fawns can follow at heel. Female offspring show philopatry and settle into home ranges on the periphery of their mother's ranges (Nelson and Mech 1981; Ozoga, Verme and Bienz 1982). This results in extended matriarchal groups consisting of socially dominant older females with several generations of daughters and their combined offspring. Daughters disperse from the matriarchal range at 2 or 3 years of age and attempt to establish their own matriarchal groups. Thus while males are cast off at an early age with little experience, females are retained within the mother's sphere of influence and disperse at a later age after they have gained in social position and experience.

In a study of dispersal in black-tailed deer, Bunnell and Harestad (1983) found that both sexes apparently dispersed as yearlings, with males dispersing somewhat greater distances than females. They reported both disperser and nondisperser individuals in the population. More work is needed to determine if the matriarchal social stature of white-tailed deer is less developed in black-tailed deer and perhaps accounts for the apparent difference in dispersal behavior between the species.

Dispersal in Social Groups with Herd Home Ranges

The second major pattern of dispersal in ungulates occurs in species with moderately sized groups with herd home ranges, such as bighorn sheep and elk. The herd structure that is required for predator avoidance allows sanctuary for young animals. These are not driven from the social unit, although once they are independent of the mother, they assume the lowest social position and are most vulnerable to predators, resource limitations, etc. In fact, the only individuals known to be excluded are those suffering from obvious injuries, perhaps because they attract the attention of predators and encourage attacks on the group, thus increasing the risk to healthy individuals (McCullough 1969). In elk, young males at sexual maturity (usually yearling age) are excluded from harem breeding groups by the master bull. The young males join bachelor groups close by. Although some young males disperse to bachelor male groups at this time, most rejoin the female groups after the rut and do not disperse to male groups until they are 2 and occasionally 3 years old. Male groups are much smaller and more fluid in membership than female groups. The largest and oldest male elk are often solitary (McCullough 1969); this is also true of bison. Males wander widely, even though they are usually found most frequently in traditional male areas (McCullough 1969; Geist 1971; Clutton-Brock, Guinness and Albon 1982). Following introductions of tule elk (*C. e. **nannodes***) in Owens Valley, California, in 1933 and 1934, within a year, bulls were seen over the full length of the valley, some 230 km, while the groups of young females remained in the vicinity of the release site. Similarly, bighorn sheep rams are observed over broad geographic areas and many habitats, while females are restricted to the traditional areas (Geist 1971, Wehausen 1980). In Owens Valley, female tule elk gradually formed separate herds centered on favorable habitat patches. Herds resist movement into unknown range; new habitat is explored, under the leadership of a dominant older female, by smaller subunits of a herd facing resource competition. If favorable habitat is located in such exploratory movements, a new herd may form due to the non-return of the exploring group to the original herd range. A new herd range is thus established which then becomes traditional. Similar budding-off of social groups in new areas occurs in bighorn sheep (Geist 1971). If suitable areas occur in proximity to existing areas, this conservative manner of dispersal works well. If suitable areas are far apart and patchily distributed, dispersal to new habitat is slow and highly uncertain.

An interesting variation in dispersal, budding off of social groups, occurs in the collared peccary (*Dicotyles tajacu*), a highly social species which holds group territories. Both sexes defend territorial boundaries against peccary groups from adjacent territories (Bissonette 1982). Feeding subgroups within the territory may occupy separate parts of the territory, rejoining only occasionally. If food conditions are favorable, subgroups spend longer times separately, and rejoining the main group is accompanied by higher levels of aggression. Thus circumstances that favor spatial segregation of feeding groups for longer periods of time also favor formation of new territorial boundaries along a line demarcating the separation of the feeding groups.

Dispersal and Large Aggregations

The third pattern of dispersal occurs in large herd-forming ungulates of open environments. Because these animals form large migratory or nomadic aggregations that move broadly about the expanses of open country, the movements of the herd perform the functional role of spatial dispersal. Thus dispersal is social and unorganized other than by mother-dependent offspring bonds and occurs between subunits of the larger herd (Lott and Minta 1983). Social bonds in caribou, bison and wildebeest are fluid and approach randomness. Thus the large dominant males that account for a disproportionate amount of mating in these highly polygynous species (Talbot and Talbot 1963, Lott 1974, Bergerud 1974a) are rather unlikely to breed with closely related females. However, in zebras (Klingel 1969), year-round family groups within the large aggregations are formed by females and offspring and a single dominant stallion. Dominant stallions defend the family group against predators (Kruuk 1972) and can be effective even against lions (Bartlett and Bartlett 1982). Young males are tolerated by the dominant stallion so long as they show no sexual behavior towards females and remain subordinate to the dominant stallion. When the maturing young stallion violates these restrictions, he is driven from the family group by the dominant stallion and joins bachelor male groups until he is old enough to compete for a family group. There is little likelihood of male offspring breeding with their own mother or full sisters.

Conversely, there is a high likelihood in zebras of female offspring breeding with their fathers because of the relatively long tenure of dominant stallions. However, when young females reach sexual maturity, they are frequently abducted by rival males and may move between several unrelated family groups before becoming a permanent member of a group (Klingel 1974). Thus females of the band are usually not closely related to one another. Rival males are not successful in abducting older adult females.

Two other species of ungulates form year-round family groups with dominant males:- feral domestic horses (*Equus caballus*) in which family groups have broadly overlapping home ranges (Feist and McCullough 1975, 1976) and vicuna (*Vicugna vicugna*) in which families occupy defended territories (Koford 1957, Franklin 1974). Similar to zebras, dominant stallions in feral horse family groups either do not defend young females from rival stallions or do so lackadaisically (Feist and McCullough

1976). In vicuna, young males approaching sexual maturity are driven out of the territorial group by the dominant male, while both he and the mother exclude young females.

Dispersal in Large Carnivores

Similar patterns of dispersal are present in large carnivores. Among species that are solitary hunters, young disperse from the home range of the mothers and wander in search of a suitable place to settle (Hornocker 1969, Seidensticker et al. 1973). Among wolves, young adult animals disperse from pack territories and usually attempt to form a pair bond with the opposite sex in areas little used by existing packs (Fritts and Mech 1981).

Dispersal in lions from prides is by young males, often brothers (Schaller 1972, Bertram 1975), perhaps because they are excluded by the adult males (Bertram 1979). After several years of wandering, they take over a pride of females where males have died or are on the decline (Bertram 1978, 1979). In wild dogs, all female young leave the natal pack and join unrelated packs (Frame and Frame 1976). In hyenas, dispersal, usually by males, is less regular, but the large clan sizes result in low probability of related individuals breeding (Kruuk 1972). Greenwood (1980) and Dobson (1982) have reported that dispersal by juvenile males is most prevalent in polygynous or promiscuously breeding mammal species, while either sex disperses in monogamously breeding species.

DISCUSSION

Lidicker and Caldwell (1982) have cogently and conveniently summarized the major questions about migration and dispersal; these questions can be addressed by the results presented here for large mammals and can be stated as the following hypotheses:

1. Migration and dispersal have a genetic basis.
2. Dispersal has an important bearing on population regulation.
3. Dispersal often precedes resource limitation.
4. Dispersal is a response to heterogeneous environments.

Results of studies on large mammals suggest that migration is not genetically controlled but rather is phenotypically determined. Tradition and the long prenatal care period allow learning through experience as the predominant factor in adaptation to a variable environment. Migration of hundreds of km over several drainages when a short altitudinal move would achieve the same end is hardly parsimonious or a likely candidate for innate control (see Baker, this volume). Similarly, cues for migration are likely learned, for even if a single cue could suffice, each individual would still have to learn to interpret the cue relative to problems presented by its own migratory pathway. Of course, genetics is involved in large mammal migration to the extent that it governs the occurence of migratory vs. sedentary behavior.

Genetic control of dispersal is modified by the social context in which it occurs in large mammals. Individual offspring may disperse voluntarily, or they may be forced to leave by socially and physically dominant animals, often their own parents. In these long-lived animals, parents must weigh (in an inclusive fitness sense) the benefits of allowing existing offspring to remain in the home area, against the cost of foregoing production of new offspring. If this equation always had the same solution, one would expect genetic fixation of behavior. Because the variables in the equation are continually changing due to the changing physical environment (resource utilization, creation and loss of habitat) and the social environment (age, strength and density of competitors), the best solution to the equation must be determined phenotypically. This is not to imply that animals decide consciously; they rather respond facultatively to current conditions and social status through physiological and behavioral mechanisms.

As to the second point, there can be no doubt that dispersal plays an important role in population regulation and adjustment of animal density to resource capacity. There is considerable evidence that high quality habitats are net exporters of animals to low quality habitats and that dispersal is the source of colonization of new habitats.

On the third point, solitary or small-group-forming species which use cryptic behavior to avoid predators are pre-saturation dispersers. Young disperse even at very low density. Group-forming species appear to be dispersers primarily at saturation, since the herd structure absorbs young animals so readily, and dispersal, when it does occur, involves socially organized groups expanding into new areas. In species that form large aggregations in open land environments, nomadic movements assume the role played by dispersal in species that associate with spatially discrete environments.

On the fourth point, Lidicker and Caldwell (1982) have reviewed the extensive literature on the relationship of dispersal to fluctuating environments. However, they also included the model of Hamilton and May (1977) on dispersal in stable environments. For large mammals, the relationship of dispersal ability to fluctuating environments seems apparent. The white-tailed deer is an excellent disperser, and dispersers are rewarded by location of recently created subclimax habitat. Bighorn sheep live in stable climax environments and are poor dispersers.

In large territorial mammals, the home area is large and discrete, and the young animal is inevitably confronted by the need to disperse. Even if the parent dies, the time of death needs to be most fortuitous for occupation of the territory by any of its own offspring to occur, and this would not help other young produced earlier in life. There is also serious doubt if young with developmental periods of a year or longer can hold the parental area from older and dominant competitors. Because an animal can only die once but can reproduce many times, dispersal is the typical case for large mammals by virtue of Malthusian population increase.

Viewed in this light the question is not so much whether to disperse or not but rather how far, and how many young are produced that need to disperse. This is true whether the environment is heterogeneous or homogenous, stable or fluctuating. Each new offspring produced by a solitary female is forced to disperse. In species which form social groups, each new young individual that is added to the population and

not balanced by death of a previous individual means one more unit of pressure for dispersal of groups to new habitat; for nomadic aggregations such pressure results in increased wandering to achieve the same quantity and quality of foraging per individual. Thus dispersal occurs as movements of individuals in species that are solitary, as increased budding-off of social groups in species with moderately-sized social groups that are spatially organized, and as greater distance of movement in species that form large nomadic aggregations. Socially the process is different, but in terms of the distribution of the population according to the availability of resources over space, the outcome is the same.

Treating dispersal as a universal "given" may clarify the question in some ways. How far to disperse in terms of population density and resource availability is related to fluctuations in the environment. In a patchy environment, wandering far in search of a new habitat patch is rewarded frequently and handsomely enough to overbalance the failure of many dispersers to find suitable conditions. In stable environments, suitable habitat is likely to be close to home, and the probability of improving success by wandering widely is extremely small. Dispersal over long distances carries additional risks of inadequate resources, increased predation, accidents and other vagaries in the unfamiliar environment. How many animals disperse is a function of birth rates and subsequent recruitment rates. Recruitment will be high in species occupying patchy environments and low in species occupying stable environments. Among ungulates, the reproductive rate per female of subclimax species is approximately twice that of comparably sized climax species, and sexual maturity is usually reached at an earlier age. Social organization and population parameters represent the suite of life history characteristics that adapt the species to the characteristics of its environment. Migration and dispersal are the short and long-term spatial elements of that adaptation.

The genetic benefits of dispersal are unclear at this time. Shields (1982) has argued that short dispersal (philopatry) occurs because inbreeding retains parental genomes that are most adapted to the local environment. This controversial view is probably a useful counter to an inadequately evaluated traditional view that outbreeding is always beneficial and inbreeding always detrimental. Determination of the degree of relatedness that is most fit in a given population must await further study. There is clear evidence in large mammals that dispersal reduces the probability of mating between highly related individuals (parent-offspring, full-sib). But there is also curiously low genetic variability in some natural populations of large mammals that have not gone through a genetic bottleneck, including moose (***Alces alces***) (Ryman, Beckman, Bruen-Petersen and Reuterwall 1977), elk (Cameron and Vyse 1978), and polar bears (***Ursus maritimus***) (Allendorf, Christiansen, Dobson, Eanes and Feydenberg 1979). This may have been due to inbreeding.

The genetic argument is likely to be long and heated (Theberge 1983, Shields 1983), and the answer is likely to be an equivocal "it depends." The dependency relates to the variable environmental circumstances that confrontgiven populations, and it should serve as a caution to remind outselves that populations adapt by simultaneous solution of genetic and environmental problems.

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EXPLORATION AND NAVIGATION: THE FOUNDATION OF VERTEBRATE MIGRATION

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ABSTRACT

Most, if not all, terrestrial vertebrates organize their movements when adult within an area of familiarity built up by exploration when younger. Many apparently unconnected movement patterns may in fact be different facets of exploration.

A crucial element in the efficiency both of exploration and of subsequent movements within the resulting familiar area is the ability to navigate. The displacement-release experiments by which navigation is studied are in effect mimics of natural exploration. Non-random orientation toward home following displacement and release has been shown for birds, bats, rodents and humans (both in Britain and the U.S.A.).

Navigation during exploration may occur both during the outward journey and at the new site to be incorporated into the expanded familiar area. An ability for magnetoreception offers particular advantages for route-based navigation in the context of exploration. Exposure to artificial magnetic fields during displacement influences homeward orientation by homing pigeons, woodmice and humans. For both pigeons and humans, applied magnetic fields may improve as well as disrupt orientation. If magnetoreceptors are based on aligned arrays of magnetic particles in tissue, improved magnetoreception may result from improved net alignment of particles in response to the applied field.

INTRODUCTION

All individual organisms are born at a site determined for them by their mother. Some time later they die at a site determined largely by their own migrations. Between these two events and places they trace through time and space a usually invisible path, their lifetime track (Baker 1978).

At first sight, the terrestrial vertebrates that are the subject of this paper present for study a bewildering variety of lifetime tracks. A useful first step, therefore, is to seek common denominators. If such exist, use can be made of the perspective generated by a comparative approach.

Accordingly, this paper has two major themes. The first is that, despite their variety, the lifetime tracks of terrestrial vertebrates while adult are nevertheless all founded on a common process of exploration and navigation when younger. The second is that the perspective to be gained from a study of human lifetime tracks can provide a powerful tool in our attempts to understand the lifetime tracks of other species.

FAMILIAR AREAS

As humans, it is our subjective experience that we organize our lifetime tracks around an area of familiarity within which, most of the time, we know where we are and where we are going. In particular, we know when and where to obtain this or that resource. Most often, also, we know the most economical route between any pair of resource sites.

Even for humans, it is by no means easy to find objective evidence for what, subjectively, we know to be true about our life within a familiar area (Baker 1982). Suitable data may be obtained from: (1) observation of the frequency with which individuals return again and again to the same site while ignoring adjacent sites of apparently equal suitability and (2) displacement-release or "homing" experiments. However, if we apply the same tests to virtually any other terrestrial vertebrate, we are likely to obtain the same results as for humans: site faithfulness and homing after experimental displacement. This should not be so surprising. Life within a familiar area has many advantages, leading, as it does, to economy of travel and efficient exploitation of available resources. With such advantages, it would be even more surprising if man were the only vertebrate to organize its movements in this way.

It is a safe assumption that all who read this paper have little seasonal pattern to their shifts of home range. There are people, however, with a distinct annual cycle to their lifetime track. Examples are some Lapps, moving to-and-fro between winter and summer home ranges in Scandinavia, and some Bedouin who traverse huge annual migration circuits within the deserts of Arabia (Baker 1978). Few readers, however, would suggest that such Lapps or Bedouin are any less familiar than themselves with the area in which they each live and move. The possibility emerges, therefore, that all terrestrial vertebrates, whether or not they show long-distance seasonal shifts of home range (e.g., McCullough, this volume), may be equally familiar with the total area in which they live. Such evidence that exists tends to support, rather than contradict, this view (Baker 1982), and perhaps few people would resist application of the familiar area model to the movements of terrestrial mammals. There may be greater reluctance to accept such a model for other vertebrates (e.g., Swingland 1983, for the Aldabran giant tortoise ***Geochelone gigantea***).

EXPLORATION

When a human or other terrestrial vertebrate is born, it has no familiar area. By the time it is old enough to reproduce, it should ideally be exploiting with economy and efficiency the resources available within a suitably large familiar area. Even for some invertebrates (e.g., social insects) information concerning unfamiliar sites may first be collected through visual, acoustic or olfactory communication with other individuals. Eventually, however, either solitarily or with others, individuals can only extend their useful familiar area by exploration: traveling beyond the current limits of their familiar area, visiting and evaluating new sites, and incorporating those that are useful within the expanded familiar area.

Exploration is a means to collection of information for future use. Indeed, an exploring animal, as it travels through unfamiliar terrain with unappraised danger and resources, is, in effect, trading the short-term disadvantages of exploration for the longer-term advantages of life within a larger familiar area.

Characteristically, vertebrates seem to be more motivated to explore as adolescents than as adults (Baker 1978, 1982). There is some evidence for rodents from breeding experiments and gonadectomy that this motivation to explore during adolescence is genetically based and hormonally mediated (Baker 1981b).

Many features of the lifetime tracks of vertebrates that at first may seem unconnected could in fact be different manifestations of exploration. The post-weaning and other "dispersals" of small mammals (Lidicker, this volume) including bats (Fenton and Thomas, this volume), "transience" (see below), and, for birds, post-fledgling and post-breeding migrations, "reversals" during seasonal migration (Richardson, this volume), and even extreme examples of downwind migration (Gauthreaux and Able 1970) can all be interpreted in terms of exploration (Baker 1982, 1984b).

Kiester (this volume) describes the behavior of a "transient" box turtle that moved through his study area. The animal moved in a more or less straight line for several weeks and eventually had traveled a few kilometers. At first sight, such behavior may seem difficult to reconcile with exploration, the latter requiring, as it does, retention of the ability to return to the original home range. Yet turtles are able to return home from several kilometers even after absences of at least several months. For example, Bertram (1979) describes a radiotracking study of a female leopard tortoise *Geochelone pardalis*, displaced 7.3 km from home and released. For 3.5 months she stayed within 400 m of the release site. Then, suddenly, her behavior changed and over a period of 53 days she traveled an indirect route of at least 12 km to return to within 50 m of the place where she was captured.

"Evidence" in support of the combined familiar area and exploration models was initially more anecdotal than experimental (Baker 1978) and some authors (e.g., Swingland 1984) have suggested that the models are, in fact, untestable (and therefore unscientific). Since 1978, however, a variety of predictions based on these models have been made (Baker 1982, 1984b). Many involve specific differences to be expected between adults and young in terms of activity, search and migration patterns

and in their use of resources. All are testable by combinations of observation, radiotracking, banding and experiment, and the first results have been published (Baker 1980a, Mather 1981).

NAVIGATION

Navigation as Part of Exploration

Exploration has three major facets (Baker 1982): (1) the exploratory migration by which the animal travels beyond its pre-exploration familiar area; (2) habitat assessment, determining which habitats are to be incorporated within the expanded, post-exploration familiar area and (3) navigation.

In the discussion that followed this paper at the Port Aransas symposium, Professor Schmidt-Koenig questioned whether, by definition, navigation could be considered part of exploration. His point was that the familiar area expands as the animal explores. At no time, therefore, is the animal beyond its familiar area. Thus, if navigation is the means by which an animal returns from unfamiliar to familiar locations, it cannot by definition be considered part of exploration.

Sometimes, of course, an animal will return from exploration by retracing its steps—pilotage rather than navigation (Baker 1982, 1984b). Except when the outward exploratory route is a straight line, however, the most economical return route will take the explorer across terrain that it has never before traveled. Thus, if navigation is the means by which an animal finds its way to a familiar destination over terrain that is unfamiliar ***in that*** the animal has never before traveled that same route, then semantically we can accept navigation as part of exploration.

Clear evidence that animals ever return home from natural exploration by navigating a direct route rather than by retracing their steps is scarce. Perhaps the most controlled data are available for geese. Led by human foster mothers, young birds walked along unfamiliar paths away from their home. When deserted, the birds rarely retraced their circuitous outward track but most often returned home by pioneering a more direct route (Saint Paul 1982). Recent advances in telemetry hold out the hope that before long we may be able to quantify how often exploring animals navigate home and how often they retrace their steps.

It is usual to view navigation in the short term as the means by which animals avoid becoming lost. Viewed in the context of exploration, however, navigation is much more than this; it is the means by which an animal pioneers the most efficient route from one resource site to another. In the long term, therefore, the efficiency with which an animal travels around within its final familiar area depends ultimately on its navigational ability. The navigational solution produced by an animal the first time it returns from a new site may not be its final solution on future occasions when more information may be available.

Displacement-release Experiments as Enforced Exploration

The usual way to study navigation is by means of displacement-release or "homing" experiments which mimic closely the behavior of natural exploration (Baker 1982). The animal is taken from its normal home range, displaced to a site it is unlikely to have visited before, then assessed for its ability to: (1) indicate the direction of home from the release site and/or (2) return home.

Examples of animals returning home after displacement and release, often over long distances, are known for a variety of terrestrial vertebrates (reviewed by Baker 1978). Relatively few species, however, have also been tested for an ability to orient in the direction of home at the release site. Yet, without such evidence, it is always possible that homing is achieved simply by chance (Wilkinson 1952).

Apart from the well-known case of the homing pigeon, examples of terrestrial vertebrates for which there is evidence of an ability to orient towards home following experimental displacement are: the turtle ***Testudo hermanni*** (Chelazzi and Francisci 1979), woodmouse ***Apodemus sylvaticus*** (Mather and Baker 1981), and bat ***Phyllostomus hastatus*** (Williams and Williams 1970). "Bus" experiments to test whether humans show such an ability after blindfolded displacement over tens of kilometers have been carried out both in Britain and the United States (Baker 1980b, 1981a, 1984b, 1985a,b, in press; Gould 1980; Gould and Able 1981).

In Britain, over 350 subjects have now taken part in over 30 bus experiments carried out by myself and my students from Manchester University. Whether analyzed by subject ($n = 372$; $e^\circ = 2 \pm 18$; $r = 0.245$; $p < 0.00001$: V-test; where e° = mean error ± 95% confidence interval in estimating home direction; r = length of the mean vector; V-test measures probability of obtaining observed homeward component of mean vector by chance; Batschelet 1981) or journey ($n = 31$; $e^\circ = 13 \pm 29$; $r = 0.509$; $p = 0.00006$: V-test), the results show a nonvisual ability to indicate the direction of home.

According to Gould (1980), initial bus experiments at Cornell by the late W.T. Keeton also "met with success," though the results have never been published for general appraisal. In contrast, Gould and Able (1981) could see little evidence of homeward orientation, either in their own bus experiments at Princeton and Albany or in the collaborative experiments between Gould and myself at Princeton. However, according to my own analysis (which avoids the "technique" employed by Gould and Able of testing multiple hypotheses against non-independent data), both of the collaborative series at Princeton and Cornell showed significant homeward orientation (Fig 1). Even if all 10 American experiments (7 at Princeton, 2 at Albany, 1 at Cornell) for which data are available are combined, the same conclusion emerges. Whether analyzed by subject ($n = 154$; $e^\circ = -1 - 50$; $r = 0.147$; $p = 0.005$: V-test) or by journey ($n = 10$; $e^\circ = 13$; $r = 0.404$; $p = 0.039$: V-test), the results show a nonrandom ability to indicate the direction of home (Fig 1).

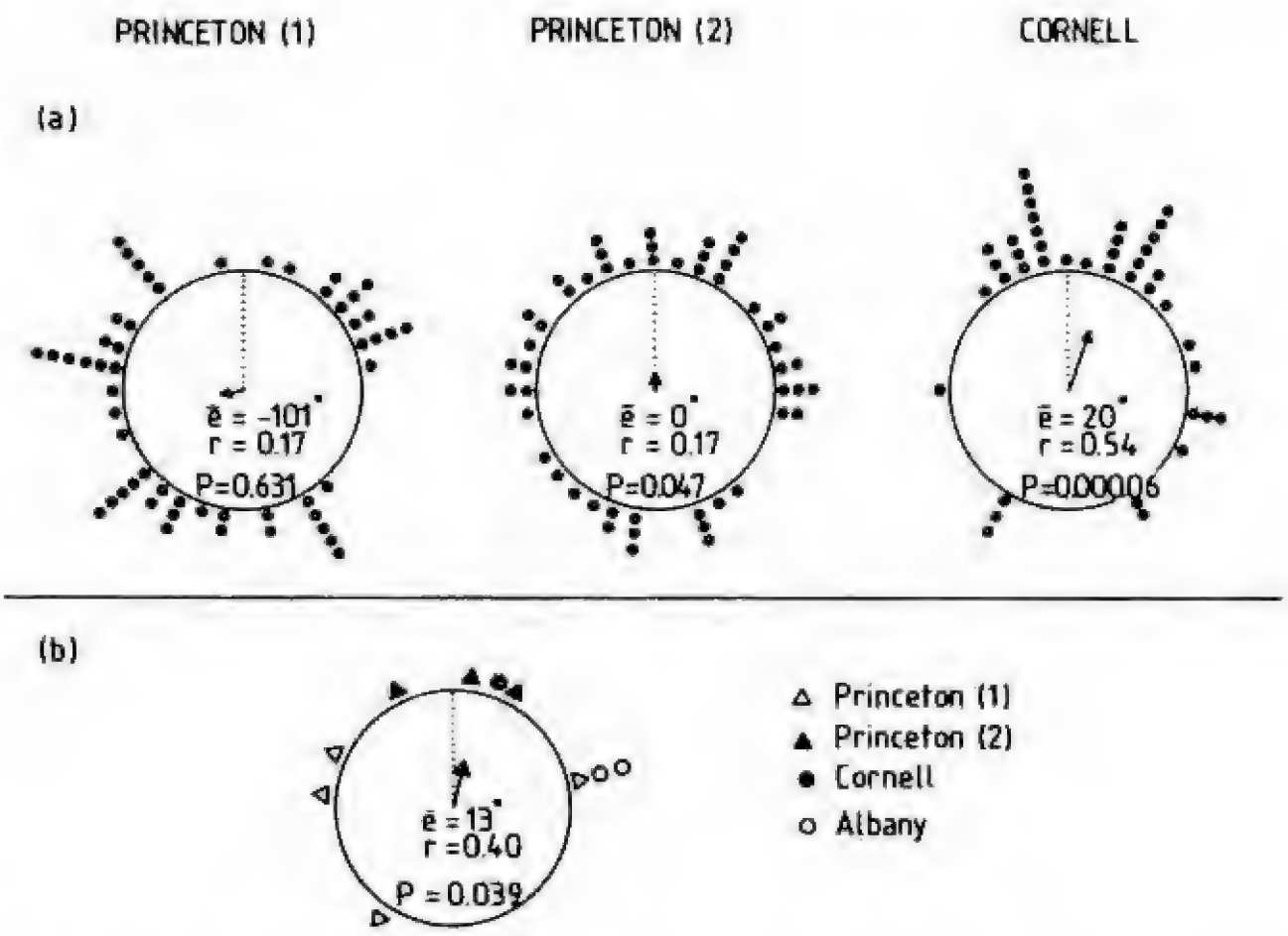

Figure 1

American Bus Experiments: (a) Individual mean errors at Princeton and Cornell. Each dot is the mean error of estimates of the compass direction of home by a subject as calculated over the 1–5 test sites on a single blind-folded bus journey. Arrow and data show the mean vector ($\bar{e}^{\circ}$, r) where $\bar{e}^{\circ}$ is the mean error of the dots shown and r is the vector length (Batschelet 1981); p is the probability that the observed homeward component of the mean vector occurred by chance (V-test, Batschelet 1981). Home direction is shown by the dotted vertical line. Princeton (1), drawn from data provided by J.L. Gould for 4 journeys in 1980; Princeton (2), data for 3 collaborative journeys in 1981 (JLG, RRB, J.G. Mather); Cornell, data for 1 collaborative journey (K. Adler, RRB, JGM). (b) Journey mean errors at Princeton, Cornell and Albany. Albany data from Gould and Able (1981).

It is interesting to note that a homeward component of about 0.15 (U.S.A.) to 0.25 (Manchester) for inexperienced humans is similar to, or even better than, the homeward component of about 0.15 for inexperienced homing pigeons from six German lofts reported by Foa, Wallraff, Ioale and Benvenuti (1982). Yet the pigeons could see while making their "estimates," whereas humans could not.

Route-based and Location-based Navigation

There are two broad categories of navigation (Baker 1981a): route-based and location-based. In route-based navigation the animal collects information during exploration or experimental displacement, thus maintaining a more or less continuous awareness of home direction throughout the journey. Location-based navigation uses information available at the new or release site. Usually, we should expect these techniques to be complementary, but if one mechanism becomes or is rendered impossible, navigation may be achieved solely by the other.

In the 1950's and 60's, studies of birds concentrated on mechanisms for location-based navigation (e.g., Matthews 1968). Since the first indication (Papi et al. 1978) from detour experiments that pigeons also use route-based navigation, more attention has been given to the latter, particularly the possible use of olfactory (e.g., Papi 1982) and magnetic information (Kiepenheuer 1978, Wiltschko and Wiltschko 1978).

Magnetoreception and Route-based Navigation

There are obvious advantages in maintaining an awareness of home direction by route-based navigation during exploration. There are also disadvantages. Not least is the mutual interference caused by the conflicting demands of exploration and navigation on particular senses. If exploration is to be adaptive, there has to be continuous vigilance, both for dangers and resources. Vision, olfaction and/or hearing will be in continuous demand. Any background navigational sense should be advantageous. At intervals, route-based navigation from this background sense may be integrated with location-based information from these other senses in accord with the various techniques for route-based navigation (Baker 1984b, Chapter 4). Magnetoreception, either to monitor the compass direction of travel or to follow the twists and turns of the journey, would seem to meet most of these demands and to be a valuable supplement to the navigational armory of any exploring animal.

Until 1981, it was assumed that artificial magnetic fields applied to animals during displacement/release experiments could only reduce homeward orientation, away from the correct direction. However in the proceedings of the International Symposium for Avian Navigation held at Pisa in September, 1981, Walcott and Gould (in Walcott 1982) reported that homing pigeons exposed to a strong, static magnetic field before taking part in a homing experiment seemed to show more accurate homeward orientation than controls. These authors suggest that the effect may be due to the artificial field influencing the alignment of magnetic particles that are hypothesized to be the basis of the magnetoreceptor—more strongly aligned particles allowing more accurate magnetoreception.

This report by Walcott and Gould has one very important consequence: until empirical results and/or our understanding of the physiology of the magnetoreceptor allow a clear prediction as to whether a particular magnetic treatment should lead to reduced or enhanced orientation, no assumptions can be made. Experiments should be designed to allow for either effect, and analysis of results should use two-tailed tests.

Manipulation of the magnetic field during the outward journey of displacement-release experiments has been shown to reduce the strength of homeward orientation by homing pigeons (e.g., Wiltschko and Wiltschko 1978; Kiepenheuer 1978; Benvenuti, Baldaccini and Ioale 1982), woodmice (Mather and Baker 1981) and horses (Baker and Panagakis, unpublished). Until now, only for homing pigeons has enhancement of homeward orientation been reported (Walcott and Gould, in Walcott 1982), though one wonders how many past experiments may not have been published ***because*** magnetic treatments improved orientation.

Navigation experiments on humans not only provide further examples of enhanced homeward orientation but also hint at a pattern consistent with the proposal (Baker 1981a, 1984a,b, 1985a; Baker, Mather and Kennaugh 1983) that the magnetoreceptor may be located in the region of the ethmoid/sphenoid sinus complex. Subjects wearing magnets on their forehead in a bus experiment at Princeton showed significant homeward orientation ($n = 20$; $e = 12°$; $r = 0.27$; $p = 0.047$: V-test) (Gould and Able 1981, p. 1061; though Gould fails to point out that the V-test yields significance) as did subjects wearing magnets on their right temple in bus experiments at Manchester ($n = 21$; $e = -11°$; $r = 0.382$; $p = 0.008$: V-test) (Baker 1985a, in press). Subjects wearing bar magnets behind the right ear on the same journeys at Manchester did not show significant homeward orientation ($n = 24$; $e = -18°$; $r = 0.216$; $p = 0.077$: V-test) nor did subjects with magnets on the back of the head, either at Barnard Castle ($n = 15$; $e = -36°$; $r = 0.323$; $p = 0.075$) (Baker 1980b) or Princeton $n = 14$; $e = -124°$; $r = 0.19$; $p = 0.715$) (Gould and Able 1981).

The good homeward orientation shown by subjects with magnets forward of the ear represents a significant improvement over that by controls wearing magnetically inert bars in the same positions ($n_{1,2} = 41$, 45; $U = 676$; $p = 0.033$ (2-tailed): Wallraff's test, Batschelet 1981, pp. 127–8). Homeward orientation by subjects with magnets behind the ear was also marginally but not significantly ($n_{1,2} = 24$, 25; $U = 313$; $p = 0.168$ (2-tailed)) better than that by controls. However, in both experiments with magnets on the back of the head, subjects with magnets showed poorer homeward orientation than controls, though even for the combined data the difference was not significant ($n_{1,2} = 29$, 28; $U = 313$; $p = 0.136$ (2-tailed)). Full details of these analyses are given in Baker (in press).

These data show that applied magnetic fields can, under some circumstances, improve homeward orientation. They also suggest that magnets exert the greatest influence on human orientation when placed forward of the ear. A similar conclusion was reached in rotating chair experiments on human compass orientation (Baker 1984b).

Walcott and Gould's report has temporarily complicated predictions of the influence of artificial magnetic fields on orientation. Further levels of complexity have been added by other rotating chair experiments (Baker 1984a, b). Not only do the results show that the position of the magnet on the head is important, they also indicate that the polarity and axis of the magnet may be equally critical. Moreover, the influence of a magnet may differ between individuals in accordance to their bed alignment (Baker 1984a).

According to Walcott and Gould's hypothesis, magnets left in position throughout a navigation experiment may exert two separate, and perhaps contradictory, influences. Not only will they alter the ambient magnetic field, they may also manipulate the magnetoreceptor to function either more or less efficiently. Walcott and Gould attempted for homing pigeons to separate these two effects by the technique of pre-treatment, exposing the animals to an artificial magnetic field before the experiment but only to the earth's magnetic field thereafter.

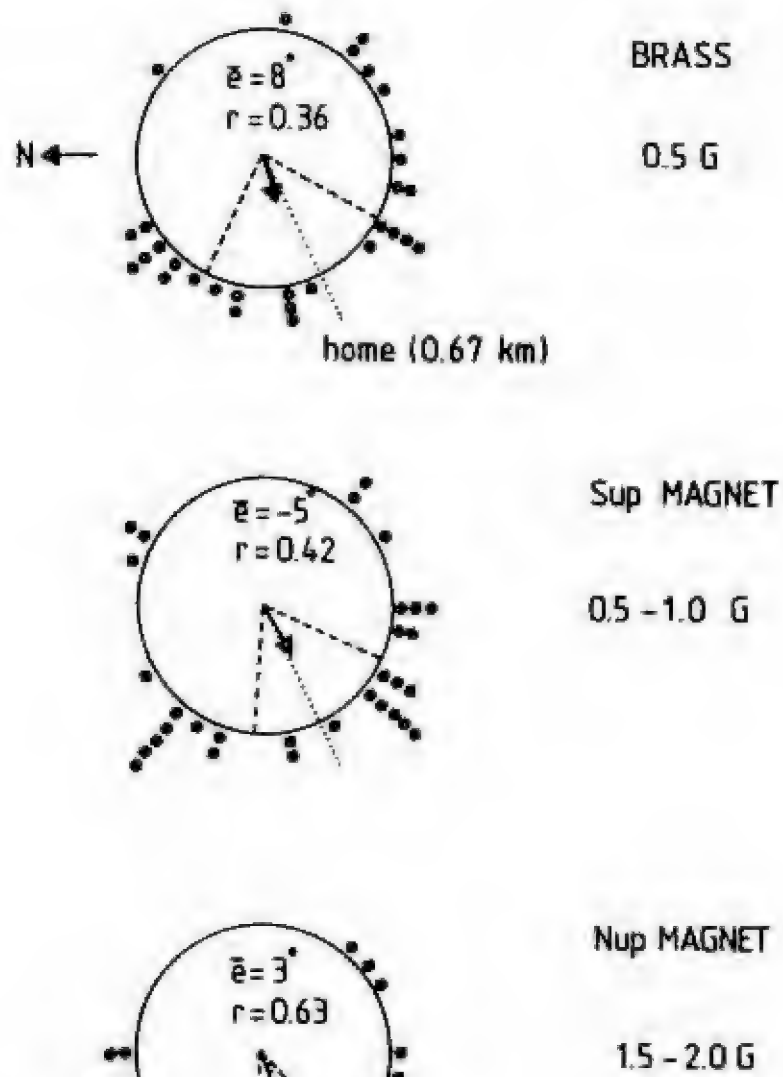

Figure 2

Influence of prior exposure to magnets on goal orientation by humans in walkabout experiments Each dot shows one subject's estimate (made by drawing an arrow) of the starting point of their journey. Although measured to the nearest degree, estimates are illustrated to the nearest 10°. Homeward orientation by subjects exposed to N-up magnets is significantly better than that by subjects exposed to brass ($N_{1,2}$ = 35, 30; U = 340; p = 0.015 (2-tailed) or S-up magnets ($N_{1,2}$ = 35,31; U = 378; p = 0.034 (2-tailed); the latter two not being significantly different (U = 414; p = 0.532 (2-tailed)) (Wallraff's test).

Pre-treatment tests on humans in rotating chair experiments have shown that a 20 mT bar magnet placed vertically between the ear and the eye for 10 minutes and then removed continues to influence compass orientation for several hours after removal (Baker 1984a,b, 1985a). In summer 1983 a series of "walkabout" experiments was carried out to test whether similar pre-treatment might influence goal orientation under conditions that approached natural exploration. In walkabout experiments, subjects are not blindfolded or passively displaced but follow experienced guides along winding paths, in this case through Gloucestershire woodland. They are allowed to use any visual or other cues they wish but are not allowed to discuss the route. None of the subjects had visited the area before; the walk therefore qualified as an exploration.

The route taken was about 3 km long and led eventually to a test site 0.67 km to the ENE of the starting point of the journey. A bar, sealed inside an opaque, brown paper envelope, was worn on the right temple 15 minutes before departure and was removed 5 minutes before the walk began. The bars were of three types: (1) brass (2) a magnet with S-pole uppermost or (3) a magnet with N-pole uppermost. All measured 77 × 15 × 6 mm and magnets had a pole strength of about 20 mT. Field strengths experienced by the subjects in the region of their sphenoid/ethmoid sinuses are given in Figure 2. At the test site, subjects were tested individually for goal orientation. Made to face a fixed direction (east) and provided with paper, clip board and pencil, they were asked to draw an arrow pointing toward the starting point of the journey. Neither experimenter nor subject knew the treatment the subject had received before the walk began.

The 96 subjects were students (19−21 years old) from the Universities of Manchester and Liverpool and were tested in three groups (June, July and September). Three major points emerge from the results shown in Figure 2:

1. Exposure to an artificial magnetic field stronger than the geomagnetic field can improve goal orientation;
2. Magnetoreception seems to be part of the navigational armory of humans during exploration even when able to see;
3. The influence of an applied field persists for at least 1.5 hours, the duration of the walk.

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KEYNOTE ADDRESS

by

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The following paper was presented as the opening and
Keynote Address of the Symposium

ROLES OF THE OCEAN IN THE EARLY SPREAD OF MAN

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ABSTRACT

The roles of the ocean in promoting or preventing the early spread of man and culture traits have been a major topic of debate in anthropology, and yet no branch of that diversified science is devoted to marine matters. Consequently, the discussions and conclusions are largely based on personal opinions or accepted assumptions. The right to pass judgement on the navigability of any stretch of open sea or the seaworthiness of any type of ancient watercraft has long been open to any theorist.

Studies and experiments conducted during a number of decades by myself and others have shown the need for a more serious and unbiased approach to research into man's early activities at sea and the role of readily constructed wash-through watercraft as a very early tool that permitted seaborn populations to engage in either planned or unpremeditated voyages more quickly and easily than any trek over large stretches of land or ice. This is a report of my own experience crossing the three main world oceans with prehistoric types of wash-through craft.

INTRODUCTION

A major problem in modern anthropology is to determine the role of the world oceans in the early spread of man and culture. It is obvious that coastlines and other open stretches of water played a leading part in determining human migration routes in the earliest ages when man still moved about as a strictly terrestrial food gatherer, compelled to alter course wherever dry land ended. In the early days before the use of either sails or wheels, ocean shores and riverbanks forced man, and sometimes lured him, along the routes that brought the human species to all continents.

But man did not forever remain a pedestrian. He became an off-shore fisherman and even a merchant mariner. His abilities to travel increased when he began to build watercraft, and he built floating vehicles before he invented the wheel. Through archaeology we know that mast and sails were in common use millennia before horse and cart. It must have been exceedingly early when man learned, like swimming animals, that by creeping up on floating wood or reed clusters he would get support, sometimes even a convenient ride.

How early our human ancestors began to build proper rafts of reeds and logs, or to hollow out the first canoe, will perhaps never be known. Crude bundle-boats for mere buoyancy were as simple to build as any shelter and did not require tools. The great steps forward were taken when watercraft were made seaworthy and navigable and permitted man to venture beyond swimming distance of the shore.

Even this step was taken very early. The first ships were in use before any major civilization developed, for the oldest civilizations have been found on islands. This is a recent and quite unexpected discovery in archaeology. A readjustment of available carbon-datings shows that the megalithic structures left on the island of Malta and certain islands around Great Britain are older than the oldest temples and pyramids of Egypt, and also that the harbor-city excavated on the island of Bahrain in the Persian Gulf antedates Sumerian civilization on the mainland.

This new evidence is as revolutionary to our understanding of the obscure human past as is the fact that man walked about on this planet two million years before any date suspected until a few years ago. What happened to our ancestors in the thousands of millennia between their appearance as a race of ***Homo sapiens*** and their reappearance as navigators and experienced architects who were constructing impressive buildings far away from any continent? How did man acquire the drive and expertise to venture out into the ocean?

We are clearly still missing important pieces in the archaeological puzzle. We have not yet quite digested the new data and taken the logical consequences. Man was two million years old when the first kingdom was founded on the banks of the Nile. Before the days of the first Pharaoh or the first dynasty in Sumer, before the existence of any scribes to record their deeds, master masons from unknown ports were crisscrossing the open seas with their families to choose widely separated island homes. These first deep-sea explorers, who escaped all documented records, had indeed spread themselves very far apart, if they had even set out from the same ports, for the islands they had chosen for their structures were on either side of the Straits of Gibraltar and on either side of the Arabian peninsula. A significant cultural evolution with considerable maritime experience must have preceded this early spread from the fertile continents to small and often barren islands off three continents.

Less than a decade ago it was generally assumed that civilization was the logical product of the favorable conditions in Egypt and Mesopotamia, where large masses of organized people had access to vast expanses of agricultural land along the banks of the river Nile and of the Euphrates and Tigris. Two civilizations, it was thought, were born during one and the same century, 3100 B.C., when land dwellers on the river banks on either side of the Arabian peninsula simultaneously invented script and started building pyramids. As long as man's age as a species was estimated at a few thousand years, it seemed natural that time was ripe for civilization to burst into full bloom in the Biblical lands of Sumer and Egypt during the very same century five thousand years ago. But then came the discovery that a third and equally fully developed civilization, also with fully developed script, settled along the banks of the navigable Indus river at the same time. First, the impressive ruins of the large cities of Mohenjo-Daro and Harappa were discovered and dated to 2500 B.C., then the older

city ruins of Amri and Kot-Diji were excavated closer to the sea and dated to just about the same century as the sudden appearance of fully grown civilization in Egypt and Sumer.

Was this remarkable triple concurrence in time, shared by the world's three oldest known civilizations, a sheer coincidence, or was it the result of earlier contact and mutual inspiration? Today we know that the chances for coincidence in time would be one in twenty thousand (one century to two-million years). In contrast, the chances for common inspiration would be great, since we know that anonymous maritime explorers with a highly developed culture had settled islands in these very same waters on either side of Asia Minor before this time. If they had found islands that far apart, they would have had no difficulties in also finding the only three large and navigable river mouths on the adjacent mainland. The art from the very earliest period of these three great and simultaneous civilizations shows that they all had ships, just like their predecessors on the islands, and all three had ships of the same rather peculiar type. In the earliest art of Mesopotamia and that of the Indus Valley, illustrations of these ships are engraved on the seals of the merchant sailors. In Egypt they are shown on the oldest pottery near the mouth of the Nile, in frescoes and reliefs of royal tombs and temples, in funeral models, and in pre-Pharaonic petroglyphs along the desert plateau between the Nile and the Red Sea. In all three areas they represent reed ships with strong curves and highly up-swung bow and stern for ocean voyaging, cross-lashings around the bundle hull, mast with sail, and one or two cabins on deck.

The remarkable resemblance between the former reed ships of Egypt and Mesopotamia have long been known, but the fact that the Indus Valley civilization also shared the same kind of vessel was not recognized until E.J.H. Mackey published his findings from excavations at Mohenjo-Daro. They included a seal showing a sailing vessel with double-mast and cabin, which Mackey properly identified as a reed ship of the same type, he says, as on the pre-Dynastic pottery of Egypt and the cylinder seals of Sumer (Mackey 1938, Vol. 1, pp. 341−342).

Another archaeologist, P. Amiet, studying the archaic glyphs which antedate the cuneiform script in Mesopotamia, found that the earliest sign for "ship" in Sumer was the same as the sign for "marine" in the earliest hieroglyphic script of Egypt (Amiet 1961, pp. 121−122). It depicts the same sickle-shaped reed boat with crosswise lashings and reeds sprawling out in bow and stern.

As is well known, the earliest Sumerians quickly changed their own script from hieroglyphic symbols to the cuneiform characters that have been deciphered. From the inscribed clay tablets of these founders of the First Dynasty in Mesopotamia, we learn that they were mariners from the time their earliest ancestors arrived by boat and established themselves at Ur, then a harbor city at the outlet of the twin rivers. Their cylinder seals consistently showed the ancestors of their divine kings navigating the sea, guided by sun and stars. The texts on a great number of their clay tablets give us details, the actual size of their ships, their carrying capacity, their cargo, and the names of distant islands and mainland kingdoms with which they carried out intensive maritime trade.

The Egyptians, in contrast, seemed rather to have settled down to become a self contained river people almost as soon as they had established their First Dynasty on the banks of the Nile. Nevertheless, on the river, the Pharaonic ships maintained the typical ocean-going lines of their pre-Dynastic ancestors such as is represented in the pre-Pharaonic art, and the successive lines of Pharaohs, like their neighbors in Mesopotamia, always depicted their earliest divine ancestry as traveling on reed boats, never on wheeled transport. That the Pharaohs descended from a maritime ancestry is rather obvious, for the rulers of the First Dynasty continued for a long time to collect taxes imposed upon distant islands in the Mediterranean Sea.

All available evidence documented in the earliest written records and illustrated in contemporary art thus concur with modern archaeology in showing that there was a very early period of maritime activity of which we are still almost totally ignorant because it antedated historic record. Historic record began with script, and ships were in use before script announced them. In other words, ships antedated the three earliest known continental civilizations. They were not, as formerly assumed, a product of these civilizations, but more likely the primary cause for cultural growth through contact and trade.

Once the three great ship-building kingdoms had been established on the banks of the three largest rivers in the area surrounding the Arabian Sea, the entire Middle East began to abound in interlocking civilizations, all with different forms of script. As suddenly, and in the very same centuries, different, equally advanced civilizations began to bloom all along the coasts of south and east Asia. For two million years or more, man had conducted a modest terrestrian life, incapable of long range trade and cargo transport, until ships gave birth to maritime nations. Once three such kingdoms, possessing both ships and script, had been established around 3100 B.C., coastal civilizations burst forth during a few centuries as far east as Indonesia and China, and west along the north African coast and out to Cyprus, Crete and other Mediterranean islands. Everywhere history took a sudden new turn. Two millennia would pass, however, before Europe was to participate in this vortex of cultural and economic growth, which finally reached Greece through sailors from Crete. The early Greeks influenced the Romans, and from the Mediterranean nations, script, art styles, architecture and all basic elements in the old Asiatic civilization finally spread throughout Europe. Another two millennia passed before the birth of Columbus who was directly responsible for the historic diffusion of all these same borrowed cultural elements to tribes and nations in aboriginal America. With the arrival of the Spaniards in Central America, a historically documented diffusion was completed. With their Bible and Cross, powder, compass, sail and rigging all inherited from Asia, Europeans introduced a new epoch to ancient civilizations in what was to become the New World.

Since the days of the great founders of religion, no single individual has set such deep traces in history as Columbus. No sea voyage since Paul the Apostle sailed to Rome to disperse Christianity throughout the world has caused such profound changes in human lives on all continents. It is understandable then that, in addition to being a time marker, Columbus seems to many to represent a sort of founder of deep-

sea ventures. We lack the names of the countless voyagers whose experience enabled them to design the sails and rigging which medieval Europe so faithfully copied in every detail five millennia later. Ship-building, maritime experience, courage, curiosity and enterprise were nothing new to mankind in the dark medieval ages when the Spaniards changed world history, nor when the Vikings wrote their sagas.

DIFFUSIONISM AND ISOLATIONISM

On these and the other points so far outlined there seem to be no dissent among modern anthropologists. Disagreement tends to abound as soon as the question arises as to whether pre-Columbian watercraft would have been able to cross from one continent to another with or against the will of the crew. When did the world ocean cease to be a total barrier for early man and instead become a principal conveyer for trade and transfer?

In some regional discussions, particularly those pertaining to the origins of civilizations in nuclear America, the views have been so conflicting that the terms "diffusionist" and "isolationist" have been coined to distinguish two ways of thinking which became almost petrified into two schools of learning. One became a diffusionist by believing that the oceans on either side of the Americas were navigable before 1492, and an isolationist by claiming that nobody could have reached or left America by sea before Columbian time.

As scientific denominations, these terms are inexact, often misleading. Who is a diffusionist, the one who plots extensive migration routes from tropical Asia to tropical America by foot the roundabout way through Siberian ice and tundra, or the one who sends them the fast way from coast to coast by boat? Any buoyant watercraft would bring drift voyagers from the Philippine Sea leisurely to northwest America with warm water in the Japan Current, not during generations but in a few weeks. Is the diffusionist route the hard one or the easy one? If the long terrestrian route by way of the Behring Strait is not diffusion, then the term diffusion applies only to maritime transfers. Yet this is not so. Easter Island, the loneliest speck of inhabitable land in the world, could only have been reached by sea. It lies 2000 miles from America and 8000 miles from Asia, yet the diffusionist becomes the one who proposes the shortest route from South America, which furthermore is a natural down-wind ride with the west-bound tradewinds and ocean currents.

Indeed, as originally defined, the term "diffusionist" should apply to one who undervalues human ability to make independent inventions, and ascribes all cultural parallels to contact; the "isolationist" unconditionally argues that the mere presence of an open ocean guarantees that no contact can have occurred prior to A.D. 1492. The roles of the ocean in promoting or preventing the early spread of man and culture traits continues to be a major topic in anthropology, and yet no branch of that diverse science is devoted to marine matters. Consequently, the discussions and conclusions have been largely based on personal opinions or accepted assumptions. The right to pass judgement on the navigability of any stretch of open sea or the seaworthiness of any type of ancient watercraft has long been open to any theorist without fear of

trespass into any person's special sphere.

This was very much the situation when, with an academic background in biology, I left for Polynesia in 1937-38 to conduct field research for the Department of Zoology at the University of Oslo. Three years of research also on Polynesian origins in the Bjarne Kroepelien Library, then as now the world's largest private book collection on Polynesia, had indoctrinated me in the general belief that only Asia could have contributed to the population of these distant islands in pre-European times. All authors agreed on this point, claiming there were no seaworthy watercraft on the American side of the ocean prior to the arrival of Columbus. Yet the problem of Polynesian origins was clearly not solved merely by eliminating America, for not two of the large number of authors who had proposed a migration route had picked the same theoretical itinerary or point of departure. With no concern for either diffusionism or isolationism, theoretical migration routes were proposed by someone, and disproven by someone else, from almost every part of Asia ranging from China to Mesopotamia and even farther beyond.

It was my original background in biology and the hardship of living one year at realistic grips with nature among aboriginal Polynesians in total isolation from the outside world that forced me to some rethinking. Reality was by no means reflected by the dots and arrows symbolizing islands and migrations on a map. The Pacific alone curves as a complete hemisphere covering half of our planet, and I had come to Fatu-Hiva, a tiny speck of land in the Marquesas Group 4000 miles from the nearest continent, America. The object of the field research was to study how biological life had spread to such ocean-born islands once formed by submarine volcanoes. Winds, currents, and transport by aboriginal man could have been the only agents of supply prior to European arrival. All the Polynesian islands are located within the tradewind belt with strong winds from America prevailing twelve months of the year. All the nuclear groups, and most notably the Marquesas first in the line, are also clustered in the main sweep of the fast current. Under these conditions it was easy to understand why the Polynesians use the terms "upwards" and "downwards" for east and west in the ocean. Upwards is the direction of America, downwards the direction of Asia. Dependent for one year entirely on an open outrigger canoe for fishing and travel, one felt the constant menace of being blown off into the powerful current which rushed like a westbound river past the coast.

Even the flora, and with it the distribution of insects and land shells, were dominated by this constant westward sweep of the elements, to the extent that most of the mountainous Marquesas islands had a moist eastern side with rain forest and a dry western side with semi-desert vegetation. What anthropologists had overlooked, but a biologist could not miss, was F.B.H. Brown's volumes on the ***Flora of Southeastern Polynesia***, from which it appears that a number of strictly American cultivated plants, the most conspicuous among them being the sweet potato, the husk tomato, the pineapple and the papaya, grew on the Marquesas islands when the Europeans came, yet none could have spread solely by winds or currents. Some of them were therefore "doubtless of aboriginal introduction." Purely from botanical evidence, Brown was led to conclude that, "undoubtedly some intercourse may have occurred between the

natives of the American continent and those of the Marquesas." (Brown 1931, 1935).

Other botanists had made similar observations on other islands throughout Polynesia, but left it to the anthropologists to draw the conclusions, and the anthropologists denied the feasibility of aboriginal arrivals from America in pre-Columbian time. But the pan-Polynesian cultivation of the American sweet potato was hard to dismiss. It was grown in Polynesia with its aboriginal South American name, ***kumara***, and was duly recorded by the European discoverers as the principal crop plant in islands as far apart as Easter Island, New Zealand and Hawaii. Together with the equally important and also pan-Polynesian bottle gourd which archaeologists began to discover in early pre-Inca tombs of Peru, anthropologists faced two cultivated plants of such basic importance to Polynesian culture that their dispersal across the ocean had to be explained. Several noted scholars then suggested that canoe voyagers from eastern Polynesia might have reached America and returned with these plants.

More numerous still were all the Polynesianists who pointed out specific American traits in the skeletal structures and blood groups of the Polynesians, or remarkable cultural correspondence between these two neighboring areas. Nevertheless, any indication of common origins or pre-European contact was explained as the result of Polynesian visits to America, or dismissed as coincidence, with a never-failing reference to the dogma that no New World people could have survived an ocean voyage prior to Columbus. There was no dissent about this claim as late as 1945 when the dean of Polynesian anthropology, the late Sir Peter Buck, published his ***Introduction to Polynesian Anthropology*** and opened by stating: "Since the South American Indians had neither the vessels nor the navigating ability to cross the ocean space between their shores and the nearest Polynesian islands, they may be disregarded as the agents of supply." (Buck 1945, p. 11).

Previously his colleague and successor at the B.P. Bishop Museum, the archaeologist K.P. Emory, had argued that it was quite within reason to entertain an American origin for a cultural element so specialized as the stone facing on Easter Island. In a subsequent publication, however, he abandoned his own view because, as he said, his colleague, the prominent Polynesianist R.B. Dixon, had pointed out to him that the balsa raft of Pacific South America quickly became waterlogged and sank (Emory 1933, p. 48; 1942, p. 129).

SOUTH AMERICAN BALSA RAFTS

Where had the Polynesianists acquired their negative attitude towards the aboriginal South American balsa raft? Certainly not from the eyewitness reports of the Spanish chroniclers who praised them in all their records. The coasts of Inca Peru had not yet even been sighted by the arriving European discoverers when they met the first Inca mariners northbound for Panama. They were encountered in the open ocean off Ecuador navigating a balsa raft against the Nino Current with twenty Peruvian men and women aboard as well as over thirty tons of precious cargo which was seized by the Spaniards. The report sent to the King of Spain by Juan de Saamanos with this booty contains a description of a very seaworthy although most unusual form of

watercraft. It was a raft with an underbody of huge logs awash in the waves but covered by a raised deck of canes so that crew and cargo remained dry. Further: "It carried masts and yards of very fine wood, and cotton sails in the same manner as on our ships. It has a very good rigging of ... henequen, which is like hemp, and some mooring stones for anchors formed liked grindstones." (Saamanos 1526, p. 196).

Advancing further down the coast, Pizarro's party of discoverers encountered fleets of the same seaworthy kind of sailing rafts in the unsheltered waters off the open coast of the Inca Empire. Some carried soldiers bound for Ecuador, others were regular merchant vessels with cargoes of precious metals and fine cloth which the Spaniards again seized to show their King even before they had set foot ashore.

This traffic of intrepid Peruvian mariners was witnessed in the Humboldt Current where it turns west straight for Polynesia. It had taken place for more than a millennium. Pre-Inca pottery vessels illustrating mariners on watercraft, and even buried boat accessories, have been excavated in vast quantities all along the open desert coast of western South America, and testify to an intensive maritime activity from Columbia through Ecuador and Peru down to northern Chile since Early Chimu and Early Nazca times. This off-shore activity was quenched by the Spanish conquest, but not until all the main chroniclers had described the impressive seaworthiness and carrying capacity of the Inca balsa rafts, which were recorded as capable of carrying up to fifty men and three horses, with both cabin and cooking place on board. Both Zarate (1555, Bk. I, Chap. VI) and Father Reginaldo de Lizarraga (1560, pp. 32, 33) wrote during the century of conquest that the coastal population of Peru were great mariners, "grandes marineros," and as late as in 1748 the Spanish naval officers Juan and Ulloa (1748, pp. 189–ff.) were able to test the navigability of the last of these indigenous balsa rafts before they disappeared from general use. They were amazed at the performance of such a seemingly primitive vessel, and wrote: "... the greatest singularity of the floating vehicle is that it sails, tacks and works as well in contrary winds as ships with a keel, and makes very little leeway. This advantage it derives from another method of steering than by a rudder, namely, by some boards three or four yards in length, and half a yard in breadth, called *guaras*, which are placed vertically, both at the head and stern between the main beams, and by thrusting some of these deep in the water, and raising others, they bear away, luff up, tack, lay to, and perform all the other motions of a regular ship."

Such historic records would seem to make it difficult to eliminate early South America as a possible contributor to the complex settlement of Polynesia, islands which are not separated from, but united to, that continent with constantly favorable winds and currents. The Polynesianists, however, did not consider it their concern to consult source references pertaining to early American history, and accepted the verdicts published by their Americanist colleagues. Actually, not many Americanists had been attracted to rafts as a topic of study. Already a century ago T.J. Hutchinson (1875, pp. 426, 454) in a paper on the "Anthropology of Prehistoric Peru" scornfully referred to the balsa raft as a "floating bundle of corkwood" and ridiculed the possibility that such a vessel could support a crew and cargo on the open ocean. This

negative attitude gradually penetrated the anthropological literature, and by 1942 it prompted the noted Inca authority P.A. Means to state with direct reference to the Peruvian balsa raft : "... it was obviously a type of boat that would awake nothing but scorn in the breasts of shipbuilders of almost any other maritime people in the world."

A major source for this gradually universal depreciation of the balsa raft was a casual remark by a nineteenth-century British traveler, G. Byam (1850, p. 200) who saw a balsa raft in full sail tacking southwards against a very strong contrary wind off the coast of Peru. Asking the captain of his own ship what it was, he was told that it was a peculiar kind of log-raft able to tack to windward with less lee-way than a European whale-boat, but made from porous balsa wood, it would absorb water and lose buoyancy in a few weeks.

Byam's reference to this alleged problem of water absorption was quoted a century later by the leading authority on aboriginal American watercraft, S.K. Lothrop. Lothrop (1932, pp. 229−256) gave a very precise description of the balsa raft and its rigging and accessories in his excellent study on "Aboriginal Navigation off the West Coast of South America", but was mislead by Byam's informant to conclude that, "balsa wood, while extremely buoyant, nevertheless absorbs water rapidly and loses its buoyancy completely after a few weeks. Owing to this characteristic, it was necessary to take the *jangada* [balsa raft] apart at intervals, haul the logs ashore, and there allow them to dry out thoroughly."

THE *KON TIKI* EXPERIMENT

These final verdicts on the balsa raft published by the leading Americanist authorities became the stumbling stone in any attempt to suggest that South American rafts might have brought South American crop plants down-wind to Polynesia more easily than Polynesian canoes could have paddled or tacked to America and returned again with plants. Confronted in the 1940's with this compact block of opposition to any thought of American sea-faring possibilities in pre-Columbian times, I saw no other way of challenging the accepted dogma than by testing a balsa raft through an empirical experiment. This was done in 1947, and with a balsa raft named KON-TIKI, manned by an inexperienced crew of six Scandinavians, the raft drifted successfully from Peru to the Tuamotu islands in Polynesia. The balsa raft covered 4300 miles or about 8,000 kilometers in 101 days, and subsequently maintained its buoyancy for a year floating in the Oslo fiord before being hauled ashore for permanent housing in the Kon-Tiki Museum. A number of lessons could be drawn from this experiment:

1. Polynesia lies within the range of aboriginal South American watercraft. It is accordingly incorrect to maintain that only Old World canoes could have entered this part of the Pacific before the Europeans came by way of South America.
2. It is true that dry balsa wood absorbs water quickly and sinks, but this does not apply to freshly cut balsa logs with sap keeping the water out.
3. It is highly unjustified to assume that the culturally advanced people of the Inca Empire maintained the use of balsa rafts for navigation because they were

backward in marine matters. On the contrary, the balsa raft survived from the earliest pre-Inca civilizations to the very fall of the Inca Empire because it was by far the most suitable of all aboriginal vessels for maneuvers in the treacherous surf over the rocks and shallows that make up the two thousand miles of completely unsheltered Peruvian desert coast. Knowing the principle of the hull from their own river canoes and from the plank-built ***dalcas*** of the Chilean archipelago, the Inca mariners had every advantage in going to sea in shallow, flat-bottomed, wash-through and navigable vessels built from the world's lightest wood, logged in Ecuador.

4. A balsa raft has more in common with a catamaran or trimaran than with a common type of raft. Balsa is lighter than cork and yet, as big logs, too strong to break in high waves or during crash landings. Broad and corky, it is steadier than any other small boat and less exposed to crashing seas than big boats because form and size leave it room to move comfortably between and over the large ocean swells.
5. The fear of foundering and the need of bailing in rough seas are eliminated on a balsa raft voyage, for the little water that enters runs out by itself through the bottom.
6. The flexibility allowed by the rope lashings, the shallow draft, and the compact logs combine to make the balsa raft the safest of all aboriginal watercraft in atoll navigation with unknown coral reefs and the only one able to carry its crew safely ashore through the towering surf on the windward reef side of the Tuamotu archipelago.
7. The space and carrying capacity for cargo and provisions greatly surpass the commodities of other small craft, and the added freedom to move about on a wide deck or inside a roomy cabin permits long voyages.
8. Marine boring worms represent a menace to wooden ships long afloat in warm Pacific waters. These organisms sank the experimental junk ***Tai Ki*** when it made a futile attempt to cross the Pacific from the Asiatic side in 1974, yet they may freely drill the balsa logs without affecting the security of a raft.
9. The feeling of complete security onboard a balsa raft sets it apart from a canoe or other small craft which will sink if waves break over the gunwales or if the bottom cracks. It also encourages the crew to venture where no other watercraft is safe.
10. The assumption that a South American crew would starve before they reached Polynesia on an unpremeditated drift voyage is unfounded. The coastal population of aboriginal Peru survived ashore by going to sea for food. In 1619 the Dutch Admiral Spilbergen (1619, p. 83, Pl. LSVII) described and illustrated a balsa raft entering Payta harbor in north Peru under full sail, maneuvered by a crew of five Indians who were raising and lowering ***guaras***. He recorded that the raft had been to sea for two months and returned with enough fish to supply all the ships in Spilbergen's fleet. Nor were the assumptions true (commonly held prior to the KON-TIKI voyage), that fish were restricted to the coastal area and that the mid-ocean between Peru and Polynesia was void of fish. A slim

and fast moving ship does not attract fish and a propeller scares them away, but a broad raft, drifting noiselessly over the surface, covered by seaweeds and barnacles, attracts marine life, and small and large fish follow along in the shade under the logs.

11. Water could be stored in any quantity desired under the raised bamboo deck where humidity and shade kept it fresh throughout the voyage. Additional supply could be obtained from rain, and a thirst-quenching liquid could be squeezed from the lymph glands of fresh fish. A noted feature in pre-Inca iconographic art is the large quantity of water jars stored under the deck of their vessels.
12. Live food plants could be carried dry in baskets on the foredeck or inside the cabin. Coconuts stored under the deck, exposed to constant splashes, lost their germinating power long before arrival in Polynesia; but coconuts and gourds stored on deck were planted with success on Raroia and Tahiti upon our landing.

The fact that Polynesia will automatically be reached by drift voyagers from Peru, without any effort of the crew, does not signify that any ocean is a conveyor rather than a barrier to aboriginal man. This depends on the respective speeds of the vessel and the water. The dead distance from Peru to the Tuamotu Islands is approximately 4,000 miles. Yet, after actually crossing only about 1,000 miles of surface water, the KON-TIKI raft reached the Tuamotu Islands from Peru. If another primitive craft had been able to travel with the same speed and in an equally straight line but in the opposite direction, it would have had to traverse about 7,000 miles of surface water to reach Peru from the Tuamotus. The reason is that the ocean surface itself was displaced about 3,000 miles, or about 50° of the earth's circumference, during the time needed for the crossing. This means that, in traveling distance, Polynesia is actually located only 1,000 miles from Peru, whereas Peru is located 7,000 miles from Polynesia, for any voyager traveling in this part of the Pacific with the speed of the KON-TIKI.

Similarly, the dead distance between Peru and the Marquesas Group is also approximately 4,000 miles, and the average westward set of the current is about 40 miles a day. This means that, if an aboriginal craft were sailing westwards from Peru with a surface speed of 60 miles a day, it would actually make 60 plus 40, or 100 miles a day, and complete the voyage to the Marquesas in 40 days. Traveling the opposite direction also in a straight line (assuming this would have been possible against the prevailing winds), it would make 60 minus 40, or 20 miles a day and thus require 200 days to reach Peru.

If, however, the craft could only make 40 miles a day, it would move west with a speed of 40 plus 40, or 80 miles a day, and still reach the Marquesas after only 50 days, but if it aimed in the opposite direction it would make 40 minus 40, or zero miles a day, and never get away from the Marquesas.

RAFT NAVIGATION WITH GUARAS

The KON-TIKI voyage was one of pure drift, and thus demonstrated only one way of possible transfer from aboriginal Peru to Polynesia. No effort was made to control the course other than by keeping the stern to the weather to ride the following seas with the sail tight. An unsuccessful attempt was made to rediscover the former system of tacking into the wind with the aboriginal system *guara* boards which we had correctly inserted in cracks between the logs. We immediately found that a new course could be set by lifting or lowering *guaras* fore and aft, but efforts to turn about and tack to the windwards, as described by Juan and Ulloa, resulted in a wild battering of the big square sail, and further trials were abandoned.

Well after the KON-TIKI drift voyage, archaeological evidence turned up in the Galapagos group which supported early eyewitness records describing aboriginal balsa rafts coming and going as the crew desired. The Galapagos group lies 600 miles from the mainland shore, on the equator and in the midst of a most treacherous vortex of currents. Two years after Byam's report of 1850, testifying that he saw a balsa raft sailing into the wind and yet spreading the heresy about its loss of buoyancy, a Swedish traveler, Captain C. Skogman (1854, Vol. 1, p. 164) also saw balsa rafts tacking to the windwards in the same area and added that the local balsa rafts were even visiting the Galapagos group.

The first archaeological survey of the arid Galapagos islands was organized in 1953 with participation of the two archaeologists E.K. Reed and A. Skjolsvold. A total of 1,961 ceramic sherds of coiled aboriginal ware, representing at least 131 different pots, were uncovered on three separate islands, besides a Mochica terra cotta flute, flint and obsidian scrapers, and a chalk-stone spinning whorl. The material, analyzed by specialists on South American aboriginal pottery at the Smithsonian Institute in Washington, was identified as originating from various cultural areas extending from the Guayas region of Ecuador and as far south as to Casma Valley on the north coast of Peru, 1,000 miles from the Galapagos. The dating of the identifiable pottery types showed that aboriginal visitors had come to these inhospitable islands since the very early period when Tomaval Plain ware and Polychrome Tiahuanacoid ware were manufactured on the coast, until the take-over of Black Chimu moulded with frog applique which immediately preceded the Inca conquest.

With only seasonal fresh water supply, a permanent settlement in the Galapagos would be difficult in aboriginal times, and the considerable number of broken vessels would suggest a repeated use of these rugged lava islands over a long period by the crew of fishing rafts, perhaps camping ashore to catch giant tortoises or iguanas.

The evidence of pre-Spanish use of the Galapagos group prompted the members of the archaeological expedition to attempt renewed experiments with *guara* raft navigation. On return to the continent, a balsa raft was built with the aid of fishermen in the bay of Playas, Ecuador, where the Ecuadorian archaeologist Emilio Estrada succeeded in locating surviving memories of *guara* navigation. With proper instructions on the critical movement of simultaneously turning the square sail and

reversing the *guaras* fore and aft, our little group of scientists managed to sail the balsa raft out of the bay and then turn about to tack back to our place of departure.

The discovery of the seaworthiness and navigability of the balsa raft inspired others to repeat the Pacific crossing, and at intervals between 1947 and 1973, no less than thirteen manned balsa rafts were launched from different ports along the former Inca coast. Two of them landed in the Galapagos group, the remaining eleven all reached Polynesia or Melanesia. Five of them, including a fleet of three balsa rafts sailing together, continued even through Melanesia and landed safely in Australia. Attempts were also made to sail pre-European types of craft across the South Pacific in the opposite direction, but none of them succeeded, and the vessels were abandoned as the crew were rescued. (Heyerdahl, 1978, Chapter 2). The Polynesian reference to east and west as "uphill" and "downhill" seems warranted for aboriginal craft in the Polynesian part of the Pacific.

REED SHIPS

The comfortable feeling of complete security on board a buoyant wash-through raft-ship directed my attention towards the second of the strange types of watercraft preferred by the coastal civilizations of Peru: the reed ship. We have all grown up with the conviction that a reed was something exceedingly frail and brittle, and the concept of riding stormy ocean waves on a boat of reeds was not in conformity with the conventional idea of boat-building impressed on our minds. Yet, as is well known, the Spanish chroniclers recorded reed-bundle boats in very common use on the ocean off the Andean coast, and regular reed ships of impressive proportions and with a full crew were seen in use contemporarily with the balsa rafts. To judge from the maritime motifs in prevalence on pre-Inca pots all along the coast, the reed boat would seem to have been more common, or at least more popular among the artists, than the flat balsa raft. Reed boats were depicted both by the potters and the weavers. Early Chimu line drawings on pots show their early divine ancestors traveling on the elevated deck of truly impressive reed ships with elaborate double stern and with the lower deck packed with people and water jars.

An archaeological expedition to Easter Island subsequent to the one to the Galapagos group convinced me of the need to revise our opinions also on the qualities of the reed ship. On this lonely island, the first inhabitable land in the open ocean off South America, early European visitors saw and illustrated small reed floats indistinguishable from those used in the coastal surf of Peru. They were made by the islanders from a fresh-water reed growing in their own crater lakes which were at first believed by botanists to be an Easter Island variety of the *totora* reed cultivated in aboriginal irrigation fields along the Pacific coast of Peru. This plant was later reexamined by the leading authority on the Easter Island flora, C. Skottsberg (1956, pp. 407, 4212; 1957, p.3) who found that the Easter Island reed was actually identical with the Peruvian species, *Scirpus riparius*, and concluded: "A direct transport of seeds across the ocean without man's assistance is difficult to imagine, and it is futile to speculate in land connections."

In the course of six months of field work on Easter Island all the expedition archaeologists uncovered representations of sickle-shaped reed ships with mast and sail. E.N. Ferdon found them as polychrome paintings in the ceiling of ceremonial stone houses at Orongo; W. Mulley found them incised on the buried part of the temple wall at Vinapu; and A. Skjölsvold and C.S. Smith found them engraved on the front of statues they excavated respectively in Rano Raraku and La Perouse Bay. (Heyerdahl and Ferdon, 1961, pp. 117, 203, 237, 239, 353, Figs. 12a, 29, 44).

Four of the older Easter Islanders still knew how to build a reed boat and proudly demonstrated how perfectly it rode the ocean waves on the windward side of the island with the four of them onboard.

The reed ships of Easter Island were made from the same reeds and with the same technique as those in ancient Peru. Apart from the notedly maritime Northwest Coast Indians of British Columbia, who navigated the sea in large double canoes remarkably similar to those of Polynesia, no American Indians, not even the Maya with their colossal dugout canoes, were as dependent on the open sea for food and transport as the coastal population of Inca and pre-Inca Peru. With timber of all sorts in the jungle of the northern and eastern parts of their empire, they preferred reeds as building material for elevated, boat-shaped watercraft, as did the founders of the great Old World civilizations. At sea these cunning marine architects forsook endurance for levity in weight and flexibility in structure, while ashore all of them quarried enormous building blocks or burnt bricks to build lasting pyramids and temple structures which continue to fill visiting tourists with awe even in our days.

As we have seen, the oldest reed ships antedate the first dynasties in Mesopotamia and Egypt. From the Middle East they spread with maritime cultures to the islands of Cyprus, Crete, and Malta, where reed ships are depicted in the ancient art, and to Corfu and Sardinia where they have survived as small craft until the present century. They even spread outside the Straits of Gibraltar, to the Phoenician port of Cadis in Spain, where three reed ships ornament a Phoenician jar recovered from the sea, and also down the Atlantic coast of Morocco, where reed ships survived in the ancient Phoenician port of Lixus until recent generations. Their early role in the spread of culture should not escape the attention of Polynesianists, as reed ships also reappear on all the outlayers forming the extreme corners of the Polynesian triangle; Easter Island, Hawaii and New Zealand. In a paper on "Traces of Reed Boats in the Pacific", K. Knudsen (1963, pp. 43, 44) shows that such important Polynesian ancestors as Kana and Lono navigated the ocean in boats made of reeds, according to Hawaiian traditions. On New Zealand such craft survived until historic time among some Maori tribes. The early Europeans saw a reed ship nearly 60 feet long abandoned on the beach (Polack, 1838, Vol. 2, p. 221), and another of the same impressive dimensions was made by the Maoris during the coronation celebration for King Edward VII in 1902, in honor of their own ancestors who had first brought them to New Zealand. (Orig. photo Canterbury Museum, Christchurch).

The falling into disuse of reed boats in Polynesia except for Easter Island, is a logical consequence of the lack of perfectly suitable reeds throughout this area, except on Easter Island where South American *totora* was grown. Along the Pacific coast of America, reed boats were seen by the first Europeans all the way from California down to Chile; they were used by the Seris Indians of Mexico until recent years but survive today in original form only on Lake Titicaca in the high Andes.

The fact that open canoes and wash-through raft-ships represented the only forms of maritime architecture in America prior to the arrival of Europeans was a standard argument against cultural influence across the Atlantic in pre-Columbian times. Nobody would come as culture bringers to America by sea, it was argued, and then forget how to build the ship that brought them across the ocean. Many observers noted the remarkable resemblance between the reed boats of ancient Mexico and Peru and those of the early Mediterranean, and this concurrence was often pointed out as one of the striking cultural parallels between the Old and the New World civilizations; but it was never suspected to be the one that had made the others possible. One of the most ardent isolationists even went so far as to pick the reed ship as an example of how even such a specialized cultural element could have been invented independently in two continents which he said were too far apart for any possible contact (Rowe 1966).

In Africa, papyrus was chosen by the ancient cultures as the reed best suited for boat-building. It was therefore surprising when the president of the Papyrus Institute in Cairo tested the buoyancy of papyrus stalks in a tank in 1969 and reported that they absorbed water, putrified and sank within two weeks. The same year I decided to build a papyrus ship, having seen that the reed-boat builders tied the ropes of their bundles tight to reduce water absorption through the cut ends. The ship was built in Egypt, the only place today with ready access to reed-boat designs showing every detail of how such vessels were shaped and rigged four thousand years or more ago. It was difficult to conceive that such complex vessels with ocean-going lines and full rigging were built if they lasted only a fortnight on the calm river. Realistic funeral decor and small models from tombs and temples showed the very special curves of the ship's body, the rope lashings, the complicated rigging to the bipod mast and the square sail, the cabin and the interplay of the double rudder-oar. The problem was that papyrus reed, once the dominant plant along the Nile, was now virtually extinct in Egypt, and the art of reed-boat building long since lost. Papyrus reeds for our experiment were therefore brought from Lake Tana in Ethiopia and reed-boat builders were imported from Lake Chad in Central Africa.

Launched in the former Phoenician port of Safi in Morocco and manned by seven men from as many nations, the 50 foot papyrus ship RA sailed for two months and had covered 2,700 miles of the Atlantic Ocean when several of the main ropes holding the reeds together were chafed off by the floor of the bamboo cabin, and most of the papyrus on the starboard side was lost in our wake, still buoyant. This mishap was due to defective construction of the elevated stern, crudely improvised in Egyptian style by the Chad boat builders who always built a flat and low stern on the papyrus vessels they used on their own inland lake.

One year later Aymara Indians from Lake Titicaca were brought from South America to Africa to build a second papyrus ship using their own technique. The Aymara, Quechua and Uru Indians of Lake Titicaca are the only boat builders in the world today that still recall the lost Middle East method of fastening reed bundles together so that the boats maintain their upright sickle-shape in stormy seas. This second test ship was built only 39 feet long, which was 11 feet shorter than the first one and 21 feet shorter than the one found on the New Zealand beach. With the same crew, now augmented to eight, RA II safely crossed the Atlantic Ocean from Morocco to Barbados, sailing 3,200 miles or 6,100 kilometers in 57 days. On both voyages the solid timber of the rudder-oars broke in storms, but the high stern on RA II protected the vessel which rode the high seas without the loss of a single reed, with bundles tough as rubber (Heyerdahl 1971).

The reed ship had been proven capable of ocean voyages, and America had been found to be located within the reach of aboriginal Old World craft. In the westward drifts of the tropical tradewind belt, America could have received impulses from Africa and transmitted impulses to Polynesia before the local presence of European craft. Our two experiments with papyrus ships had been pure drift voyages. Small and very heavily loaded, RA II had become completely saturated long before arrival in America, and was too deep in the water to be easily navigable, although it remained afloat with no risk for lives but with considerable inconvenience for crew and cargo. Obviously these elegant ships with the complicated rigging had not been designed by their creators for mere drift voyages such as ours, so the original reed boat navigators must have known a method for keeping their vessels high and dry in the seas.

Egyptian texts had little to say about their ships although the art abounded in detailed illustrations of ships and rigging. The Sumerians, in contrast, were rather cursory in their ship representations but recorded a wealth of information on their clay tablets. From their written records we learn that, when a big reed ship was built, a blend of six ***sar*** of pitch, three ***sar*** of asphalt and three ***sar*** of oil went into the melting pot. There are numerous references to large vessels of reed, termed ***ma-gur***, which first brought the Sumerian ancestors to Mesopotamia and later served as merchant vessels carrying cargo back and forth at will from distant lands.

In spite of these written records, modern scholars remained as prejudiced towards the Sumerian reed ships, which were built from the local ***Typha aungustata***, as they had been towards vessels of balsa wood or papyrus reeds. The ***Typha*** reed of Mesopotamia, like the papyrus of Egypt, had been tested and found to absorb water and sink. The leading authority on Mesopotamian ships, A. Salonen (1939, p. 70), in his otherwise excellent and most exhaustive study of Sumerian and Babylonian watercraft, shows that in the earliest Sumerian period the large ***ma-gur*** were built from reeds, yet he assumes that ocean navigation could not start until the Sumerians learned to import wood for planked ships because the ships of ***Typha*** reeds "unquestionably" had to be brought ashore to dry out after use.

Visiting the present-day Marsh Arabs, who live in the reed swamps of Iraq where the Sumerians formerly built their reed ships, I learned that reeds retain their buoyancy if cut in the month of August. In 1979, the Aymara Indians who built RA II were brought to Iraq, and assisted by Marsh Arabs, they built a ***ma-gur*** of local ***Typha*** reeds, 18 meters or almost 60 feet long. With a multinational crew of eleven men and loaded with provisions for half a year, this Sumerian type reed ship was navigated independent of winds and currents for five months, and was still undamaged and riding high on the waves at the termination of the testing. Built from untreated ***Typha*** reeds cut in August, the reed ship ***Tigris***, named after the river into which it was launched, sailed down the Shatt-al-Arab to the open Gulf, visited the island of Bahrain, navigated through the difficult Hormus Strait and sailed south to Muscat in Oman, then turned and sailed northeast to Pakistan; from Karachi the voyage went straight from Asia to Africa across the Indian Ocean, to terminate in Djibouti at the entrance to the Red Sea (Heyerdahl 1980).

CONCLUSIONS

The combined lesson from these three ocean crossings is that a sounder, more empirical approach to the study of the role of the oceans in the global spread of man and culture is needed. A full understanding of the capacities of early types of watercraft concerns biologists as well, whether the problem confronted is the spread of spinnable cotton, the gourd, the domestic dog or parasitic hookworms. In the brief timespan of our own generation, replicas of pre-European watercraft manned by inexperienced crews have managed to cross the three world oceans once assumed to have represented insurmountable barriers for such vessels. It seems unrealistic to assume that nothing similar might have happened during the millennia of formative cultures and fully developed civilizations that preceded the European epoch in world history.

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CHAPTER FIVE

BIRD MIGRATION

Many generalizations about animal migration have been strongly biased by discoveries from investigations of bird migration. This undoubtedly stems from the tremendous interest that birds generate because of their conspicuousness and their remarkable abilities of flight. The ecological, physiological, and behavioral aspects of bird migration continue to attract considerable attention from investigators, and many of the new and exciting contributions from recent studies are summarized in this section of the proceedings.

In my contribution, I have attempted to order the diversity of avian migration strategies by concentrating on climatic changes in time and space and how such changes influence the absolute amount of resources in the environment. The variance in the ability of animals to secure sufficient resources in response to different patterns of resource decline is related to the patterns of bird movement at different temporal and spatial scales. This exercise helps to relate bird migration strategies to the spectrum of animal migration strategies.

The theme of intraspecific variation in bird migration is continued in the contribution of Ketterson and Nolan. They summarize their important work on the partial and differential migration of the dark-eyed junco (***Junco hyemalis hyemalis***) and report new results on how well the patterns of zugunruhe (migratory restlessness) in caged juncos of different sexes and ages relate to data on the actual timing and distance of migration in this species. The importance of endogenous and exogenous factors in the regulation of the seasonal migration of birds is addressed in Berthold's contribution. Berthold presents considerable evidence that suggests that endogenous programs (that are in part heritable) control migratory disposition and many other aspects of the migratory activity in birds. A comparison between Berthold's paper and that of Ketterson and Nolan offers the reader a modern day example of how earlier investigators were lured into the "nature" vs. "nurture" controversy that raged some thirty years ago.

The orientation of birds during migration has been an area of intensive investigation since the seminal experimental work of Gustav Kramer in the late 1940's and early 1950's. The paper by Able and Cherry summarizes the recent advances in field observations and experimental studies and illustrates just how exciting and dynamic this area of research is. The role of various compass mechanisms is evaluated, and evidence is presented that suggests that some compass mechanisms have little or no role in the orientation of migratory birds. In another contribution on orientation, Bingman, Beck, and Wiltschko emphasize the complexity of the

development of orientation systems in migratory birds. They summarize their studies of the development of migratory orientation in the pied flycatcher (***Fidedula hypoleuca***), a European-trans-Saharan nocturnal migrant, and demonstrate that young birds are able to use either the geomagnetic field or the night sky as "primary" sources of directional information for migration.

Two papers in this section are based on migration data gathered with the use of radar. The influence of weather on the day-to-day variation in the numbers and types of birds migrating over southeastern Canada is discussed by Richardson. He also addresses the orientation of the birds in flight and the routes that birds following during migration in relation to wind patterns. The second paper is contributed by Alerstam who monitored with tracking radar the flight behavior of arctic terns (***Sterna paradisaea***) and common terns (***Sterna hirundo***) during migratory flights across Sweden. The flight behavior of both species is detailed first and then Alerstam examines the flight behavior in relation to fuel economy and energy budget. Such considerations must relate back to the distribution and abundance of resources, and having come full circle that is where we will begin.

Sidney A. Gauthreaux, Jr.

THE TEMPORAL AND SPATIAL SCALES OF MIGRATION IN RELATION TO ENVIRONMENTAL CHANGES IN TIME AND SPACE

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ABSTRACT

Because habitats change in suitability and resource availability through time, birds that have specific habitat requirements with regard to these measures must change location and seek new habitats elsewhere if they are to survive and reproduce. The spatial movements of birds, whether maintenance, dispersal, or migratory, are evolutionary strategies that express the expectations of temporal change in conditions at the present locality. If the resources in a suitable habitat can support a certain number of individuals during a period of high resource availability and only a fraction of that number during a period of low resource availability, than during the latter period, some of the individuals in the population must move and seek other suitable habitats or perish. The climatic and meteorological factors responsible for changing the suitability and resource availability of a habitat through time may be in large part the same factors that shape the spatial and temporal characteristics of movements from or to that habitat. Climatic changes can influence the spatial distribution of suitable habitats and the absolute resource availability within suitable habitats and by doing so influence either directly or indirectly the direction and distance of the movement patterns. Likewise climatic changes can dictate the heterogeneity of habitats in time (length of favorable and unfavorable periods, and length of time a location remains suitable) and influence the phenology (timing and rate) of the movements. The diversity of avian migration strategies can be related to the diversity of environmental changes that occur over different temporal and spatial scales.

INTRODUCTION

Because habitats change in suitability and resource availability through time, birds that have specific habitat requirements with regard to these measures must change location and seek new habitats elsewhere if they are to survive and reproduce. The spatial movements of birds, whether maintenance, dispersal, or migratory, are evolutionary strategies that express the expectation of temporal change in conditions at the present locality. If the resources in a suitable habitat can support a certain number of individuals during a period of high resource availability and only a fraction of that number during a period of low resource availability, then during the latter period some

of the individuals in the population must move and seek other suitable habitats or perish. The climatic and meteorological factors responsible for changing the suitability and resource availability of a habitat through time may be in large part the same factors that shape the spatial and temporal characteristics of movements from or to that habitat. Climatic changes can influence the spatial distribution of suitable habitats and the absolute resource availability within suitable habitats and by doing so influence either directly or indirectly the direction and distance of the movement patterns. Likewise, climatic changes can dictate the heterogeneity of habitats in time (length of favorable and unfavorable periods and length of time a location remains suitable) and influence the phenology (timing and rate) of the movements. In the paper that follows I show how the diversity of avian migration strategies can be related to the diversity of environmental changes that occur over different temporal and spatial scales.

RESOURCE AVAILABILITY, RESOURCE HOLDING POTENTIAL AND THE PROBABILITY OF MOVING FROM A HABITAT

The level of resource availability in or the favorableness of a suitable habitat can fluctuate greatly. Resource availability can be absolute (the amount of resources in a habitat) or relative (the actual resources available to an individual in relation to other individuals in the population). Absolute resource availability (ARA) is an attribute of the habitat, while relative resource availability (RRA) is an attribute of the individual and related to its resource holding potential (RHP). For a given level of absolute resource availability in a habitat, the relative resource availability may be different for each individual in the population. The absolute resource availability within a habitat and the resource holding potential of an individual in a population occupying that habitat are important in determining the probability that an individual will have to move from the habitat to secure sufficient resources elsewhere. The ARA of a habitat and the RHP of an individual require some additional explanation.

Absolute Resource Availability (ARA)

The ARA lines in Figure 1 are isoquant lines, each indicating a constant quantity of absolute resource availability in a habitat. The slopes of the isoquant lines are related to the amount of resource encountered as a function of area sampled. Isoquant line ARA_0, for example, indicates that no resources are in the habitat. Isoquant lines $ARA_{0.1}$, $ARA_{0.5}$ and ARA_1 indicate increasing amounts of resource as a function of area sampled. Isoquant ARA_∞ indicates that resources are infinitely abundant. Although the latter case is unrealistic, it is precisely the same as saying the carrying capacity is unlimited. Thus the series of ARA isoquant lines in Figure 1 illustrate a whole function of the two variables: amount of resource and size of area sampled. Each isoquant is associated with a particular value of absolute resource availability, and the array of isoquant lines represents an isoquant map.

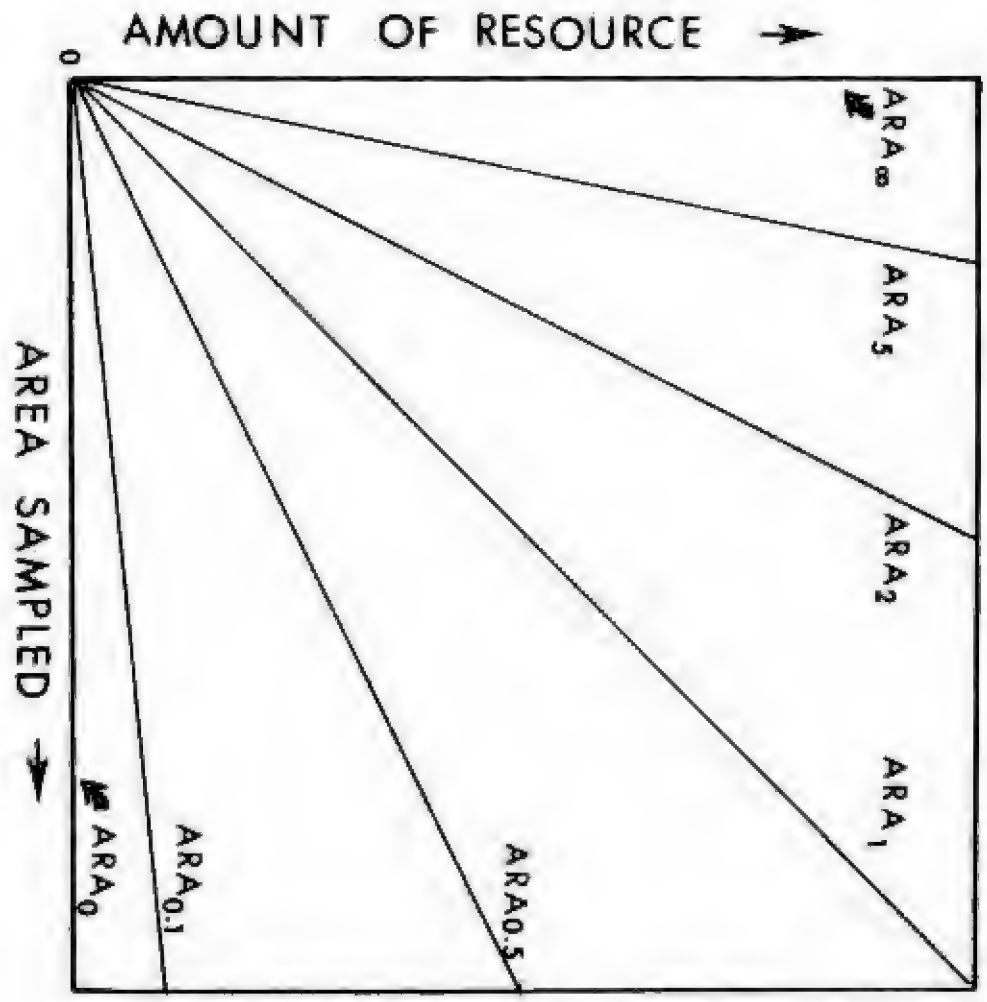

Figure 1

An isoquant map of absolute resource availability (ARA) in a habitat. Each isoquant line represents all the possible combinations of area sampled and amount of resource found for a particular absolute resource availability.

Resource Holding Potential (RHP)

Individuals in a habitat rarely share resources equally. Given a certain level of absolute resource availability, some individuals acquire more resources than others. In other words, the relative resource availability differs from individual to individual, unless the absolute resource availability is unlimited. The factors responsible for one individual acquiring more resources than another are related to game theory (Maynard Smith 1976). If resources in a habitat are limited, the individuals in a population that occupy that habitat will compete (engage in contests) for access to the resources. Most contests are asymmetrical (Parker 1974), because individuals vary in fighting ability or resource holding potential (RHP), and the value of the resource to the contestants (expected payoff) often differs. The RHP of an individual depends on a number of factors (e.g., size, age, sex, strength, weaponry, physiological condition and experience). When the RHP of two individuals are similar, a contest may escalate for a brief period until one individual has assessed the RHP of the other. However, in most cases individuals are able to assess asymmetries in RHP without resorting to overt aggressive behavior (Gauthreaux 1981). In the latter case, the individual with the higher RHP acquires the resource, and the individual with the lower RHP does without and seeks the required resource elsewhere. Consequently, when the absolute amount of resources in a habitat decreases, individuals with relatively high resource

holding potential may be able to secure enough resources and remain in the habitat, but other individuals with low RHP's may have to move from the habitat or perish because sufficient resources cannot be secured (see Baker 1978, pp. 68, 402–406; Gauthreaux 1978).

The relationship between an individual's resource holding potential and its probability of moving from a habitat is presented graphically in Figure 2. Because this relationship is sensitive to the absolute resource availability in a habitat, the ARA isoquant map of Figure 1 has been included in the graph. The orientation of the isoquant map in Figure 2 is turned 90° counterclockwise relative to Figure 1, because of the convention of having the indiependent variable (resource holding potential) increase along the abscissa and the dependent variable (probability of moving) increase along the ordinate. The relationships among the isoquants are nonetheless identical to those in Figure 1.

According to Figure 2, when the absolute resource availability of a habitat is unlimited (ARA_∞), all individuals in the population can remain in the habitat regardless of resource holding potential. The area sampled in the habitat to obtain adequate resources can be infinitely small (cf. Fig 1). This situation is of course unrealistic. As the absolute amount of resources in the habitat declines (isoquant ARA_2), individuals with the lowest RHP will have the highest probabilities of moving. When the absolute resource availability is further reduced (isoquant $ARA_{0.5}$), half of the individuals in the population must leave the habitat to secure resources elsewhere. Of the individuals that remain in the habitat, even those with relatively high RHP must sample large areas to secure sufficient resources (cf. Fig 1). When the absolute resource availability reaches zero, no individual can remain in the habitat and survive. Thus the amount of resource in a habitat ultimately controls the number of individuals that can stay in the habitat, and the fluctuations in the absolute amount of resource influence the number of individuals that must move from the habitat. With this in mind it is possible to elaborate the various avian migration systems as a function of different temporal fluctuations in the environment.

AVIAN MIGRATION STRATEGIES

Migration in a general sense encompasses all movements in space that an individual makes in response to changes over time (Baker 1978, Gauthreaux 1980), including maintenance, dispersal, and migratory movements. In this interpretive overview only the last two types of movement are considered, but maintenance movements (e.g., foraging movements, roosting movements) could be included by emphasizing smaller temporal and spatial scales of environmental change.

The type of movement pattern shown by some or all of the individuals in a population depends in large part on the frequency and amplitude of environmental fluctuations that cause variability in the absolute resource availability of a habitat. The variability in the absolute resource availability of a habitat can be attributed to two distinct sources. One source is from processes ***internal*** to the habitat that involve interactions of organisms with one another (biomass production and consumption), and

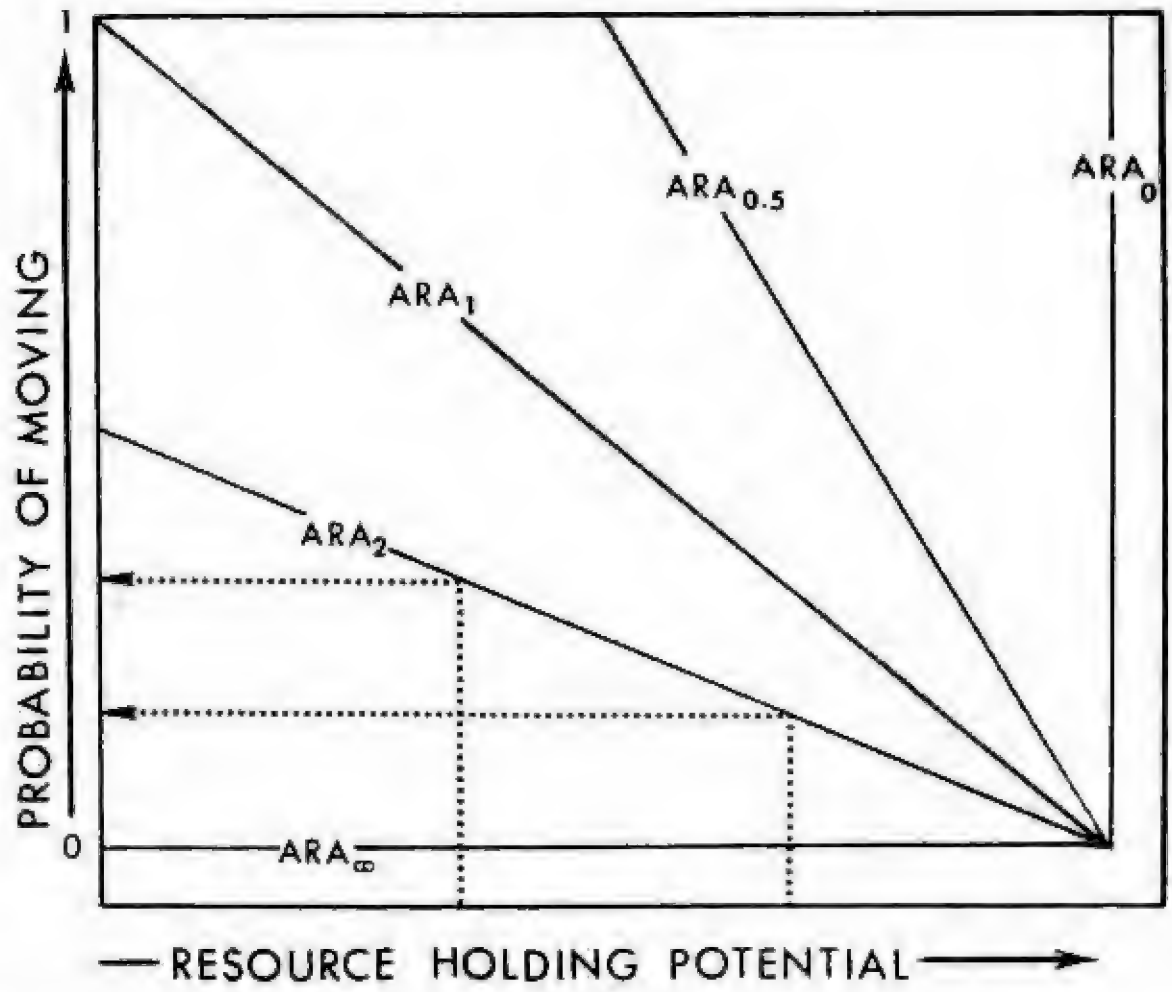

Figure 2
The graphical relationship between resource holding potential and the probability of moving from a habitat for different absolute resource availabilities (ARA's).

the other source is from processes *external* to the habitat that involve environmental events or changes that are independent of the state of the habitat. Although the internal processes are important and can be evaluated when external processes are more or less constant, the external processes are forcing mechanisms and strongly control internal system variability. Consequently the time scale of external events (environmental changes) favors resonant amplification of internal events (changes in absolute resource availability) on the same time scale, with an appropriate lag. Mitchell (1976) has presented a variance spectrum of climatic variability that spans all time scales of variability from one hour (10^{-4} years) to the age of the earth (4×10^9 years). Three sharp peaks in the relative variance of climate occur at periodicities of 1 day, 1 year and 100,000 years. These three peaks correspond to the diurnal cycle, annual cycle and the quaternary ice-volume cycles. With reference to avian migration systems, the annual climatic cycle has by far the most important influence on internal events within the habitat.

Because of the overwhelming influence of the annual climatic cycle, many habitats show distinct annual periodicities in absolute resource availability. The amplitude of the fluctuations in ARA varies greatly depending on the geographical location of the habitat, and it is the amplitude of the annual fluctuations in absolute resource availability that ultimately influences the migration patterns of birds occupying a particular habitat (Fig 3).

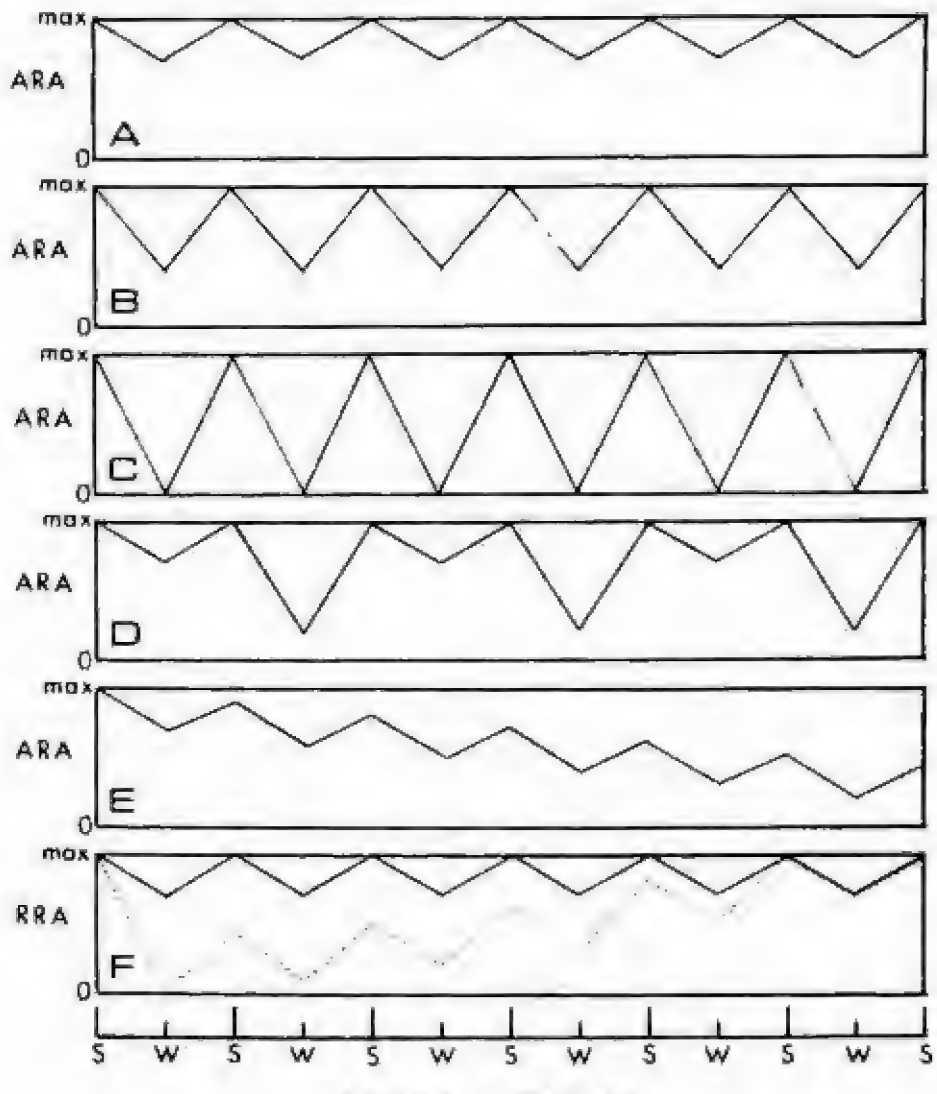

Figure 3

Patterns of annual fluctuation in the absolute resource availability (ARA) and the relative resource availability (RRA) of a breeding habitat. S = breeding period, W = nonbreeding period. See text for further explanation.

Breeding and Natal Dispersal

The distribution of a population is inevitably more patchy than the resource distribution, even if the resource distribution itself is random (Roughgarden 1977). Thus dispersal enhances the chances that an individual with a low RHP in its natal habitat will find a suitable habitat in which to survive and reproduce. Because available habitats are randomly distributed, the orientation of dispersal movements may be random for the population as a whole.

The temporal pattern of dispersal movements is dependent on fluctuations in resource availability over time. Because birds should reproduce when their breeding habitat is at its maximum level of resource availability, dispersal movements occur just prior to breeding (breeding dispersal of adults) or just after breeding (natal dispersal of young). The former movements are spacing processes by which the available habitat is divided among potential claimants, and individuals that have found a place to settle may, by their behavior or by their presence alone, cause other individuals to look for a settling area elsewhere (Brown 1975, p. 50). The final distribution of the individuals in the occupied habitat is known as the dispersion

pattern of the species (Brown and Orians 1970). Natal dispersal occurs just after breeding as the level of absolute resource availability begins to decrease in response to increased population size and the annual climatic cycle (Fig 3A). In birds, dispersers are usually young females with comparatively little resource holding potential in their natal habitats (see Greenwood 1980). Through dispersal they may find new habitats where they can avoid intense competitive interactions, secure enough resources to survive, increase their resource holding potential through maturation and experience, and ultimately breed. Once these processes have occurred, an individual shows strong site tenacity (reluctance to leave the habitat). Thus once an individual has achieved high resource holding potential, it is unlikely that it will have to leave a habitat or a certain location within a habitat, unless the absolute resource availability declines to levels where survival is in jeopardy. If an individual with high RHP must vacate its breeding habitat (or nonbreeding habitat for that matter) during periods of low or zero ARA, it will likely return to the habitat (show site fidelity) once resource levels increase. For birds, return movements are not characteristic of dispersal, but they are quite typical for migratory movements (see Gauthreaux 1982).

Partial Migration

When the annual fluctuation in absolute resource availability of a habitat is great, but sufficient resources remain in the habitat during the nonbreeding period to permit the survival of a portion of the population, only those individuals with relatively high resource holding potential can remain in the habitat (Fig 3B). Those individuals with lower resource holding potential must move to locations where they can secure enough resources to survive during the period of low ARA. This pattern of movement is called partial migration, and the individuals that must leave the habitat during the period of low ARA usually return to the habitat from which they departed when the level of ARA increases. Because age and sex are important determinants of resource holding potential, for most species the migrants are young, and in those species where males are dominant to females, the migrants are largely female (Lack 1954, Gauthreaux 1978, Greenwood 1980).

Complete Migration

When the annual fluctuation in absolute resource availability of a breeding habitat is so great that resource levels reach zero during the nonbreeding period (Fig 3C), no individuals can stay in the breeding habitat, and all must move to locations where resource levels permit survival. In this case the distance of movement may be related to the resource holding potential of an individual, such that those individuals with the highest RHP move the shortest distance and those with the lowest RHP move the longest distance (differential migration, but see Ketterson and Nolan 1982 and this volume). When all individuals migrate approximately the same distance, RHP may determine the relative quality of the nonbreeding habitat. In both of these cases individuals with the highest RHP would tend to arrive earliest in the breeding habitat

once absolute resource levels increase (see Gauthreaux 1978).

Irruptive Migration and Nomadism

When the annual fluctuation in absolute resource availability of a habitat is different from year to year (Fig 3D), the type of movement from the habitat differs from year to year. Only dispersal movements may occur during a year with a minor decline in resources, but the following year when resource levels decline sharply, a large portion of the population must leave the habitat to seek resources elsewhere. In the latter case the movement is called irruption (Lack 1954, pp. 227–242; Bock and Lepthien 1976), and the individuals that move from the breeding habitat are those with low resource holding potential (Baker 1979, pp. 634–635). The alternation of movement patterns is coupled with a circumboreally synchronized pattern of seed crop fluctuations in certain high-latitude tree species, and these fluctuations are possibly related to the quasi-biennial cycle of climatic variability (Mitchell 1976) that is harmonically related to the annual change in climate.

In theory, when the absolute resource availability shows strong year-to-year fluctuations in a breeding area, site tenacity should not be adaptive, and nomadism should be a more profitable strategy. This situation has been examined by Andersson (1980), and he concludes that nomadism in birds is a better strategy with cyclic than with random fluctuations in absolute resource availability, and the advantage of nomadism increases with the interval between successive good years in an area.

Biogeographic Migration

Thus far the annual fluctuation in the absolute resource availability of a habitat has been stressed (Fig 3 A–D), but fluctuations in absolute resource availability can and do occur simultaneously over time periods of considerably greater length (longer wave lengths). The latter fluctuations affect not only the absolute resource availability of a habitat but also the nature of the habitat itself through long-term successional changes (Fig 3E). Over successive generations, maximum resource availability in a habitat may steadily decline so that eventually the habitat is no longer suitable for reproduction. Through annual dispersal movements, habitats that are more suitable may be found, and eventually the range of the species will shift so that long-term faunal migrations will track long-term floral migrations (see Gauthreaux 1980, 1982).

DIFFERENTIAL MIGRATION AND RELATIVE RESOURCE AVAILABILITY (RRA)

Thus far the emphasis of this paper has been on the absolute resource availability (ARA) within a habitat and how a pattern of decline in ARA influences the pattern of movement of a part of or the whole population from that habitat. In this section, I wish to emphasize the relative resource availability (RRA) to an individual and how this may influence the migration strategy of that individual. The relative resource availability is that portion of the absolute resource availability within a habitat that is available to an individual because of its resource holding potential relative to that of other individuals occupying the habitat or location (Fig 3F). Even when the absolute resource availability within a habitat is high, for an individual with relatively low resource holding potential, relative resource availability is low. Figure 3F illustrates the relative resource availability (RRA) to an adult and to a young bird of the year over successive annual climatic cycles. During the first nonbreeding period (W) the RRA declines only slightly for the adult, but for the young of the year the RRA declines sharply. During subsequent breeding and nonbreeding periods the difference in RRA between the adult and the maturing immature decreases, so that after several annual cycles, no difference exists. This pattern is fundamentally similar to that found in a number of seabird species (Dunnet et al. 1979). The pattern can apply to other species as well, (e.g., gannet ***Sula bassana***, white stork ***Ciconia ciconia***, osprey ***Pandion haliaetus***, Manx shearwater ***Puffinus puffinus***), but depending on the species, the number of annual cycles needed before an individual acquires a high resource holding potential and hence a high relative resource availability will be less.

The spatial extent of movements of individuals from a breeding location are manifestations of the differences in relative resource availability at the breeding location. For many bird species during the nonbreeding season the youngest individuals in the population are distributed the farthest away from and the adults are closest to the breeding location. The distance from the breeding location that an individual overwinters is determined by its resource holding potential in relation to the absolute resource availability of a location such that ***it will have a high relative resource availability for survival***. Even though an individual may have a low resource holding potential, if it can find a suitable habitat with few or no individuals with higher resource holding potential, it will enjoy a relatively high resource availability and be able to survive. Thus individuals with high resource holding potential can move relatively short distances from breeding locations (or not at all) and secure sufficient resources for survival during periods of reduced absolute resource availability, but individuals with low resource holding potential may have to move considerable distances before they can find a location where the relative resource availability is high enough for survival. The data in Figure 4 are from a month-by-month analysis of banding returns of herring gulls ***Larus argentatus*** from the Great Lakes of the United States (Moore 1976). In November when climatic conditions are still relatively mild, all age classes are recovered near the breeding grounds. As

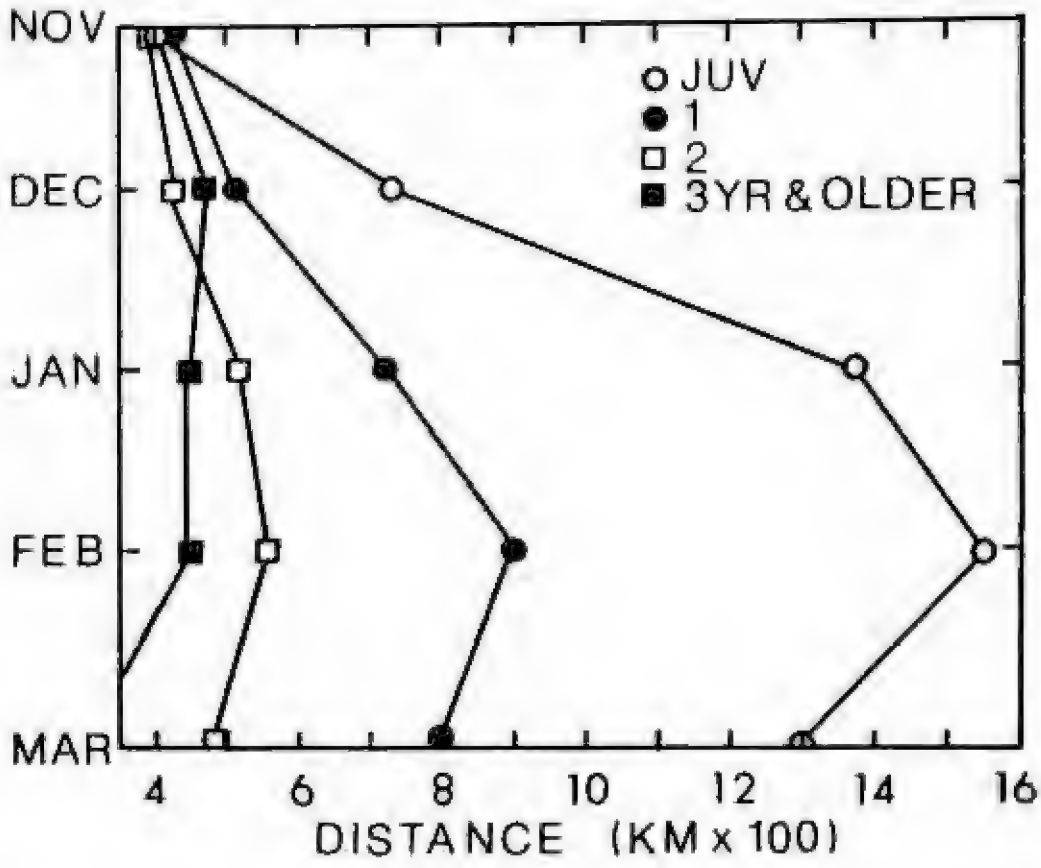

Figure 4
The age dependent migration distances of herring gulls in relation to monthly climatic changes. (Modified from Moore 1976).

winter progresses, the age classes show greater segregation with maximum segregation occurring in early February. Once climatic conditions improve in March, all age classes move toward the breeding grounds because the amount of absolute resource availability within the breeding areas is increasing. The axis of movement should generally follow the climatic gradient and be perpendicular to the isotherms, because of the relationship between the severity of climate and absolute resource availability.

CONCLUSIONS

The amount of resource in a habitat ultimately controls the number of individuals that can occupy a habitat, but the fluctuations in the amount of resource influence the number of individuals that must periodically move from the habitat. Thus, the spatial movements of birds, whether maintenance, dispersal, or migratory, are evolutionary strategies that express the expectation of temporal changes in conditions at the present locality. It is the nature of the temporal changes that dictates the type of spatial movement that an individual will show.

Temporal changes in resources can be attributed to processes ***within*** the habitat (resource production and consumption, habitat-organism feedback) and to processes ***outside*** of the habitat that involve environmental changes that are independent of the state of the habitat. Because external processes are forcing mechanisms, the time scale of external events (environmental changes) favors resonant amplification of internal events (changes in absolute resource availability and all the covarying biological events) on the same time scale with an appropriate lag. Thus habitats may

fluctuate asynchronously in favorableness or absolute resource availability because of stochastic biological events (different population levels in different habitats), but synchronous changes in favorableness or absolute resource availability may also be superimposed on these habitats by widespread, deterministic climatic events (daily and annual climatic cycles).

When habitats fluctuate in favorableness asynchronously, a dispersal strategy will be adaptive, but when synchronous fluctuations in favorableness occur, a migration strategy will be adaptive. The type of migration pattern (partial, irruptive, short- or long-distance) shown by a species will depend on the amount of decrease in the absolute resource availability within the habitat. The individuals that stay (if any) and the individuals that leave during periods of reduced resource availability within the habitat will depend on certain attributes of the individual and the absolute resource availability within the habitat. The individuals with high resource holding potential and high dominance status will perceive high relative resource availability and will be able to remain in a habitat with low absolute resource availability. Those individuals in the population with low resource holding potential (and consequently experiencing no relative resource availability) will have to move as far as necessary to locate a habitat where they too can experience a relative resource availability that will permit survival.

Although differences in the resource holding potential of the ***individuals*** in a population have been emphasized as being important proximal factors in the incidence of migration, the same factors may be applied to differences in migratory behavior between species. O'Connor (1981) has shown that migrant-resident differences are significantly related to body size differences, such that the larger species show a high competitive ability to exploit resources during the breeding season and that the smaller migrant species are primarily exploiters of breeding season resources under-exploited by a resident population held down by winter mortality (see also Herrera 1978). Thus asymmetries in RHP such as size may be as important to species differences in migration as it is to individual differences in migration.

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LABORATORY AND FIELD STUDIES OF AVIAN MIGRATORY ORIENTATION

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ABSTRACT

This paper will review recent advances in field observations and experimental studies of migratory orientation in birds. Most work is based on the assumption that nocturnal migrants possess a sun, star and magnetic compass, but these capabilities have been certainly demonstrated in very few species. Visual information from clear skies around the time of sunset has emerged as an important cue in the orientation decision in a number of night migrants. Birds in orientation cages respond to manipulations of both the position of the sun and skylight polarization patterns, but the relationships of these cues to one another and to other potential directional stimuli are unknown. A growing but by no means unanimous body of orientation cage data supports a primary role for the magnetic compass in the selection of migratory directions and in the calibration of other cue systems. Field observations have revealed no strong evidence of magnetic involvement in the orientation of free-flying migrants where wind often produces strong effects on flight direction. In light of these developments, the role of stars in the migratory orientation process has become much less clear.

INTRODUCTION

Current investigations of the migratory orientation of birds are proceeding on several fronts: (1) radar and visual observations of free-flying migrants, (2) experiments employing wild-caught migrants in orientation cages and (3) experiments designed to reveal and manipulate the ontogeny of orientation behavior during early development. Elsewhere in this volume Bingman, Beck and Wiltschko discuss the latter area of research, whereas we will concentrate on the first two. We have made no attempt to provide an exhaustive review of the literature; rather we will focus on areas in which recent advances have been made and on problems and questions that seem in need of resolution.

Over a decade ago, Emlen (1971) emphasized the important distinction between selection of a migratory direction (decision-making) and the maintenance of that direction once aloft during the migratory flight. Although the same stimuli might function in both contexts, it is useful to employ this conceptual dichotomy, and my

discussion will follow that scheme. It has become axiomatic, at least in the field of bird orientation, that multiple, sometimes redundant, cues are involved in migratory orientation. Much recent work has focused on the interactions among potentially usable orientation information. Especially in migratory species, less work has recently been directed toward the discovery of new orientation capabilities, but we should not lose sight of the possibility that all pieces of the puzzle may not be before us.

DIRECTIONAL DECISION-MAKING

Most of us are willing to accept that at least some bird species possess a sun compass, star compass and magnetic compass. It is worth noting, however, that much of the evidence marshaled in support of a star compass was inferred on the basis of appropriate orientation performed by birds exposed to clear night skies. The demonstration of a magnetic compass rendered those results inconclusive. Thus we are now in the uncomfortable position of having unequivocal evidence of an independent star compass in only a very small group of species (the sylviid warblers studied initially by Sauer (1957), Sauer and Sauer (1960); and the indigo bunting ***Passerina cyanea*** (Emlen 1967a,b)). Indeed, only in the case of the indigo bunting do we have extensive data on the mechanism and development of the stellar orientation mechanism (Emlen 1967b, 1970).

Ironically, documentation of the more recently discovered magnetic compass now exists for a considerably larger list of migrants (four species of ***Sylvia***, European robin ***Erithacus rubecula***, indigo bunting (see Able 1980), savannah sparrow ***Passerculus sandwichensis*** (Bingman 1981a), pied flycatcher ***Ficedula hypoleuca*** (Beck and Wiltschko 1981)). Thus there are two species, indigo bunting and garden warbler ***Sylvia borin***, in which the present data support the existence of both star and magnetic compasses. Whereas many of us tend to assume that such capabilities exist in many species, we must recognize that such generalization is built on a very small foundation.

Given these capabilities, what does a bird actually do when it sets about to make a decision concerning which way to fly on a given night? In orientation cages under clear starry skies, Wiltschko and Wiltschko (1975a,b) found that several species of European night migrants changed orientation in a predictable manner when magnetic directions within the cages were shifted by means of Helmholtz coils. Although there are some problems with the interpretation of these experiments (see Able 1980, p. 331), they suggest that magnetic information is primary in this situation, overriding stellar cues in the choice of direction. These experiments were based on the premise that magnetic and stellar cues were the predominant if not the only cues involved in the migratory orientation of these species. In this sense, the birds may have been presented with an unrealistic task.

Field observations have shown that nocturnal migration commences with an explosive exodus during the dusk period when other visual cues (e.g., position of sunset, landmarks on the ground) are available. The orientation decision may well be made at that time or, perhaps more likely, even earlier during the transition between

daylight and darkness when the bird is still on the ground (Vleugel 1954, Emlen 1980). A host of recent studies has revealed major effects of stimuli available around the time of sunset on the orientation of typical nocturnal migrants.

One type of experiment involved testing birds in orientation cages under two conditions: (1) exposed to the clear sky around the time of sunset and tested until well after stars became visible and (2) placed in the cages only after all traces of sunset glow had disappeared. The first and most extensive of such experiments were those of Moore (1978, 1980), but the basic result has now been replicated in several other species (Table 1). Two consistent effects are evident. Birds exposed only to stellar cues are more likely to hop less or not at all during the tests. More important, orientation of individuals is much poorer, the directions selected are more often inappropriate, and pooled means from a series of tests are usually not oriented. At least two of these species can perform appropriate orientation under stars alone (savannah sparrow (Bingman 1981b) and white-throated sparrow ***Zonotrichia albicollis*** (Able, unpublished)), but the difference in the quality of orientation when exposed to the clear sky at sunset is quite dramatic and suggests that cues available at that time, but not after dark, are of considerable importance in the directional decision.

That the relevant information for dusk orientation is visual has been shown by Moore (1982) who shifted the sunset orientation of savannah sparrows in the predicted manner by employing mirrors attached to windows in the sides of an octagonal palisade surrounding the orientation cages. Experiments with European robins tested indoors in the presence of a single light source suggest that the sun itself may be a sufficient stimulus to yield seasonally appropriate orientation (Vilks, Katz and Leipa, in press). However, clear sky at sunset contains patterns of polarized light that are directly related to the position of the sun. Pigeons had been conditioned to discriminate between rotating and stationary polarized light and between widely separated stationary *e*-vectors (Kreithen and Keeton 1974; Delius, Perchard and Emmerton 1976), but the behavioral relevance of this ability was unknown. Able (1982a) showed that the orientation of white-throated sparrows during the time between sunset and the first appearance of stars could be manipulated by altering the axis of skylight polarization visible to the birds in orientation cages. Similar results have been obtained with American tree sparrows (***Spizella arborea***) (Able, unpublished). It is as yet unclear exactly how skylight polarization interacts with other cues in migratory orientation—whether as an indirect means of sun compass orientation as in honeybees (***Apis mellifera***), simply as an indicator of sunset position for menotactic orientation, or in some other way.

Taken together with observations of free-flying migrants described below, these results point to the period of time around sunset as one of major importance in the decision making process among nocturnal migrants. It is appealing to think that information from a variety of sources is integrated at this time and that calibration of one orientation cue system by another might take place. As yet the precise relationships are unknown. Based on the results obtained later in the night by the Wiltschkos and experiments by Viehmann (1982) which indicated that migratory

Table 1

Comparison of the pooled orientation of several species of nocturnal migrants tested when exposed to clear sky at sunset and stars after dark (SS/ST) and when exposed only to starry skies after complete darkness (ST).

Species/Season Source	Number of Tests SS/ST, ST	Mean of Means or Modes SS/ST	*r*	Mean of Means or Modes ST	*r*
Savannah sparrow, spring (Moore 1980)	66, 31	352°	0.771*	75°	0.327 ns
Savannah sparrow, fall (Moore 1980)	15, 15	209	0.803*	214	0.322 ns
White-throated sparrow, fall (Bingman and Able 1979)	34, 17	170[1]	0.910*	347[1]	0.280 ns
White-throated sparrow, fall (Lucia and Osborne 1983)	8, 3	174	0.898*	279	0.866 ns
American tree sparrow, spring (Cherry and Able, unpublished)	81, 17	292[1]	0.750*	238[1,2]	0.390 ns
European robin (Katz, in press)	37, 15	240	0.490*	65	0.195 ns

*Significant by the Rayleigh test.

[1] These values are means of the modes of individual tests of birds. All other values in these columns are means of individual test means.

[2] ST tests of this species were performed within a set of Rubens coils which were not activated.

r = the length of the mean vector.

directions were selected before nightfall on the basis of magnetism, it is important to ask how magnetic and solar information might be related. Bingman (ms) has been able to predictably shift the sunset orientation of dunnocks (***Prunella modularis***) by altering magnetic directions with Helmholtz coils, but we have been unsuccessful in inducing similar shifts in American tree sparrows tested from sunset until after dark (Cherry, unpublished).

Radar and visual observations of well-oriented migratory flight under solid overcast skies and of the response of migrants to wind direction were partly responsible for the development of the notion that birds must be using several independent cues in orientation. Recent observations of migrants in the field have also yielded a picture that is in many ways coincident with the results from orientation cages described above.

Emlen and Demong (1978) released and tracked white-throated sparrows during twilight at Wallops Island, Virginia. The sparrows headed in an appropriate northward, spring direction under clear skies, suggesting a possible role of sunset information. At the same coastal locality during a period of prolonged solid overcast, the flight directions of the migrants became increasingly spread. A break in the cloud cover late in the afternoon of the third day of continuous overcast afforded a view of the sun and sunset in the local area. On that night, orientation was dramatically improved, but tracks became more dispersed during the next two days as overcast solidified again (Emlen 1980). These data are consistent with the hypothesis that visual information present under clear skies at sunset is of crucial importance in the selection of migratory directions.

Radar tracking studies of free-flying migrants in upstate New York have revealed relationships among celestial cues and wind direction (Able 1978, 1982b). Able tracked birds early in the evening on nights when winds were opposed to the normal direction of migration for the season. When skies were clear, affording a view of both sunset and stars, migrants headed in the expected direction for the season. When solid cloud cover prevented them from seeing both the sun in the late afternoon *and* the stars at night, they headed downwind and thus oriented in an inappropriate direction for the season. On a few nights when cloud cover prevented a view of either the setting sun *or* stars but not both, the behavior of the birds was indistinguishable from nights when skies were clear during both afternoon and early evening. This pattern points to a primacy of celestial cues over wind direction in this inland region and suggests that either sun-related cues *or* stars is sufficient to allow birds to make an appropriate directional decision. In the absence of these visual cues they rely on wind direction. We have obtained parallel results from white-throated sparrows released from balloon-borne boxes and tracked by radar. On clear nights with light but opposing winds, sparrows wearing frosted lenses headed downwind, whereas birds with unimpeded vision oriented primarily in the seasonally appropriate direction (Able, Bingman, Kerlinger and Gergits 1982). In addition, these data and those of Larkin (1980) suggest an ability on the part of flying birds to determine wind direction even under conditions in which visual references are very limited or absent.

Whereas some studies of migratory orientation in cages have suggested a primacy of magnetic information, there is no evidence from field observations that magnetism is involved in directional decision making. Richardson (1976) reported a statistically significant counterclockwise shift in the mean heading of migrants arriving over Puerto Rico in autumn with increases in the intensity of natural magnetic storms. Moore (1977) found a positive correlation between dispersion in flight directions observed by ceilometer and *K*-values in the southeastern United States. The biological significance of these findings is not clear, and other studies have failed to reveal such relationships (Able 1974, Richardson 1974). The lack of strong, consistent evidence of magnetic involvement in the orientation of free-flying migrants remains the most notable inconsistency between orientation cage studies and field observations.

MAINTENANCE OF ORIENTATION IN FLIGHT

Detailed observation of nocturnal migrants en route have shown that birds do not simply choose a direction and maintain it mechanically. On the contrary, birds aloft respond in complex ways to the environment around them and to the air through which they are moving.

One of the most consistent conclusions to emerge from radar and visual studies is that random flight directions or tracks of apparently disoriented birds are very rarely observed. Once a directional decision has been made and birds are aloft, the presence of solid cloud cover above them seems to have remarkably little effect on their orientation (Able 1982c). Observations on other effects of overcast have been less consistent. Birds tracked while apparently flying within clouds or between cloud layers have sometimes been disoriented as a group and have flown significantly less straight than individuals under either clear or solid overcast skies (Able 1982c), but this has not always been the case (Griffin 1973). Likewise, long-duration unbroken cloud cover has sometimes been associated with disorientation among night migrants (Hebrard 1971, Emlen 1980) or with increased scatter in tracks (Steidinger 1968), but Able (1982c) did not find this to be the case in two separate instances so long as the birds were flying beneath the cloud deck.

Whether and to what extent birds are drifted by lateral wind components has long been controversial. Alerstam (1976) has reviewed the situation and shown that there are cases in which birds probably experienced uncorrected drift and others in which complete compensation was evident. Between these extremes lies a large region in which distinguishing between uncorrected wind drift and selectivity of different winds based on different preferred track directions (pseudo-drift) involves several assumptions. In the northeastern United States, night migrants flying over inland areas often seem to be drifted from the predominant southwesterly flight direction observed on calm nights. By making simultaneous observations at three sites in upstate New York, Bingman, Able and Kerlinger (1982) showed that night migrants apparently responded to a major north-south river by changing their headings so as to compensate at least partially for wind drift when flying in strong cross-winds. In other wind conditions, no differences in orientation were observed near and away from the river. In Switzerland, Bruderer and his colleagues (Rüsch and Bruderer 1981, Bruderer 1982) have also found selective influences of landmarks upon orientation. There was a tendency for birds flying over the rugged terrain of the Alps to be influenced by topographic features under totally overcast skies, regardless of wind direction. Under both cloudy and clear skies, birds migrating in potentially drifting winds responded to local topographic leading lines in a manner that countered wind drift. Alerstam and Pettersson (1976) found that several species of birds migrating across the Baltic Sea in autumn seemed to use waves in an attempt to compensate for wind drift, treating the waves as stationary landmarks and thus drifting with them.

This sort of variability in the responses of migrants to wind in flight is probably to be expected, and we should not expect a unitary answer to the wind drift question. Alerstam (1981) has outlined a variety of strategies regarding wind drift and compensation, including circumstances when it might be advantageous for migrants to allow themselves to be drifted. Williams and Williams (1978) have explored one such situation, the trans-Atlantic migration of birds from North to South America. Movements made up of both waders and passerines depart from New England and the Maritime Provinces of Canada on northerly to westerly post-frontal winds. Data from shipboard and land-based radars throughout the western Atlantic indicated that the birds maintained an approximately constant southeastward heading throughout this vast journey, first drifting eastward far out over the ocean, then westward on the easterly trade winds into the continent (but cf. Richardson 1980 and this volume).

TRENDS AND PROBLEMS

What discernible trends emerge from these disparate data? The importance to the orientation decision of visual information which is available around the time of sunset and during the time period immediately prior to the initiation of nocturnal migration has become a major theme. At the same time, the role of the star compass and its relationship to other directional cues has become less clear. It appears at the moment that much of the selection of a migratory direction occurs when stars are not visible, and their absence rarely results in disruption of oriented flight. It may be premature to propose that their primary function is only that of celestial "landmarks" used to maintain a pre-selected direction, but it is apparent that a careful look at stellar orientation in a variety of species is in order.

Although many of the classic criticisms still pertain (recently repeated by Griffin 1982), a growing but by no means unanimous body of data supports a primary role for the magnetic compass in the selection of migratory directions and in the calibration of other cue systems. If the results presented by the Wiltschkos (1975a,b, 1976) are relevant to other species, we may expect considerable variability in terms of how and when the magnetic compass is consulted by migrants. Orientation on the basis of visual cues which are calibrated by the magnetic field at one time may carry over for a period of time during which magnetic re-evaluations are not made. An experimental change in the magnetic field during this period will produce no effect or perhaps a delayed response on the part of the birds. The existence of such time lags would greatly complicate the design and interpretation of experiments and introduce enormous variability into attempts to detect magnetic involvement in the orientation behavior of migrants in the field. It is discouraging, but perhaps not surprising, that less noisy, more easily replicated results have not been forthcoming.

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PHYSIOLOGY AND GENETICS OF AVIAN MIGRATION[1]

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ABSTRACT

When one considers the available information on the physiology and genetics of avian migration, a typical migrant (especially a long-distance one) can best be described as functioning via a series of endogenous and in part heritable programs. A fundamentally endogenous system of circannual rhythms related to the entire migratory behavior initiates and terminates migratory events as an internal calendar. Synchronizing photoperiods produce seasonal precision. Migratory activity has actually been proven to be a heritable, species- and population-specific characteristic, related to the distance a bird has to travel. In this sense, inexperienced juvenile migrants are thought to fly in innately prescribed migratory directions as long as their endogenous migratory time-program dictates and as a result reach their specific winter quarters "automatically" (vector-navigation hypothesis). Fuel for migration seems to be provided in a similar way: endogenous programs control migratory disposition, hyperphagia, fat deposition and dissimilation along with other aspects of migratory activity. The seasonally appropriate amount of fuel appears to be guaranteed by an endogenous, sliding set-point mechanism of body weight control. Concerning partial migration, the innateness of the migratory urge in partial migrants has recently been demonstrated experimentally. Maintenance of both migratory and nonmigratory individuals within the population is therefore due to a balanced polymorphism. Its potential evolutionary rate appears to be fast. Although considerable progress has been made with respect to the formal description of endogenous and genetic components involved in the physiology of avian migration, our knowledge of the true nature of circannual rhythms and the role played by neuroendocrine systems is still limited.

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INTRODUCTION

Generally, the field of the physiology of avian migration includes possible external and internal control mechanisms, e.g., photoperiodic influences, endogenous rhythms of various types including endocrine cycles and specific metabolic functions, as well as processes of sensory physiology related to spatial orientaton. There is not the remotest chance to treat all these features in the space available in this paper, and thus I will concentrate on some selected topics that have been the focus of our research in Germany on Old World warblers, mainly of the genus Sylvia. I will concentrate on (1) the occurrence and significance of internal calendars, (2) the endogenous control and heritability of migratory activity, (3) the innateness of the migratory urge and its implications in partially migratory species, (4) the so-called vector-navigation hypothesis, and (5) the control of habitat preferences related to the course of migration.

METHODS

The main methods on which our studies rely are: (1) handraising nestlings and the subsequent investigation of migratory events in various experimental conditions, (2) cross-breeding and selectively breeding birds in aviaries for about 10 years, and (3) studying the course of migration at three large bird trapping stations spread over middle Europe (Lake of Constance, southern Germany, Hamburg, northern Germany, and Lake Neusiedl, Austria). Measuring migratory activity displayed as nocturnal migratory restlessness in registration cages has also played a major role. Restlessness was automatically recorded with movable perches mounted on microswitches. For a review and more details see Berthold (1975, 1977).

RESULTS

Circannual Rhythms: Occurrence, Significance, and Synchronization

We now know that for a group of migrant species (*Sylvia*), "*Kaspar Hauser*" animals, which live in constant experimental conditions without any seasonally changing environmental cues, are still seasonally well organized. An example is given in Figure 1: a young garden warbler (*Sylvia borin*) that hatched in May and was handraised and kept in a constant daily light : dark ratio of 10:14 hours with constant temperature, air humidity and food supply, began its juvenile molt at the end of June—at the appropriate time for freeliving conspecifics. While still molting, body weight began to increase due to heavy fat deposition. During this period of rapid weight gain, nocturnal migratory activity, so-called migratory restlessness, developed. Hence the bird had spontaneously become a typical migrant. Later, and at about the right time, the following events occurred: fat dissimilation and body weight decrease, cessation of migratory restlessness, winter molt and later the entire sequence of events for homeward migration, the next autumn migration, and so on. Between the

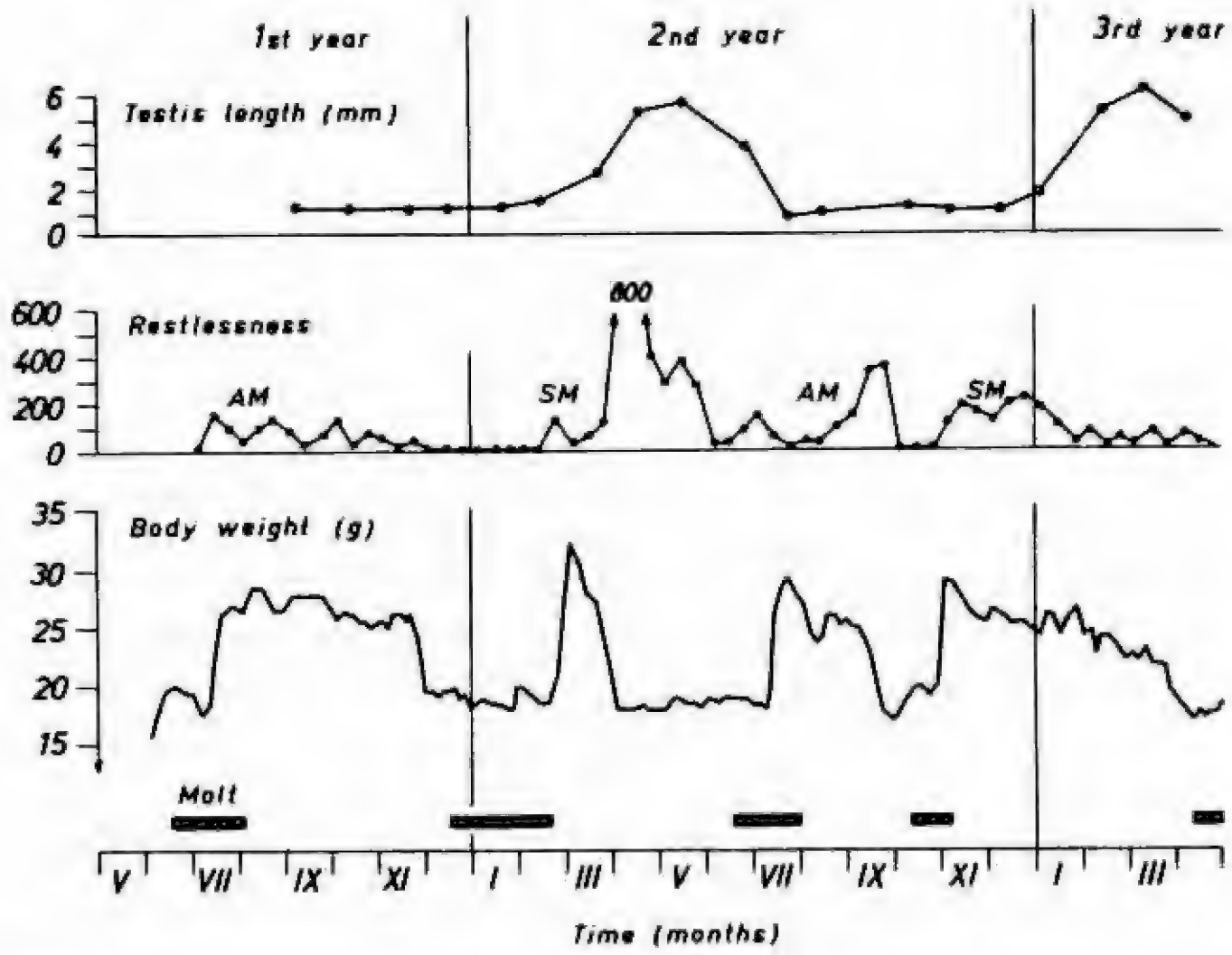

Figure 1

Circannual rythyms of four annual events in an individual garden warbler, kept in constant conditions (daily light : dark ratio 10:14 hours) from the juvenile development onward during a long-term experiment. AM, SM, autumn, spring migratory period. From Berthold et al. (1971).

migratory seasons, the gonads developed and regressed. There is, however, a remarkable difference between the data for this individual and its freeliving conspecifics: the events of the 3rd and 4th migratory season occurred clearly earlier than in the wild, indicating that the underlying endogenous rhythms ran faster than the calendar year. That is the reason that this type of biological clock with a period length of about ten months is called "circannual rhythm" derived from circa and annual.

We were able to maintain some individual warblers in constant exerimental conditions for a period of over ten years, proving that the observed circannual rhythms were true biological clocks: self-sustained, freerunning, and of life-long efficacy. Figure 2 shows a long-term body weight and molt curve in a garden warbler kept for 10 years. Body weight cycled continuously, alternating with molt and heavy fat deposition up to the end of the ninth experimental year. These results of long-term studies demonstrate that endogenous annual clocks are basically involved in the control of seasonal migratory events and that they persist life-long even in "*Kaspar Hauser*" animals.

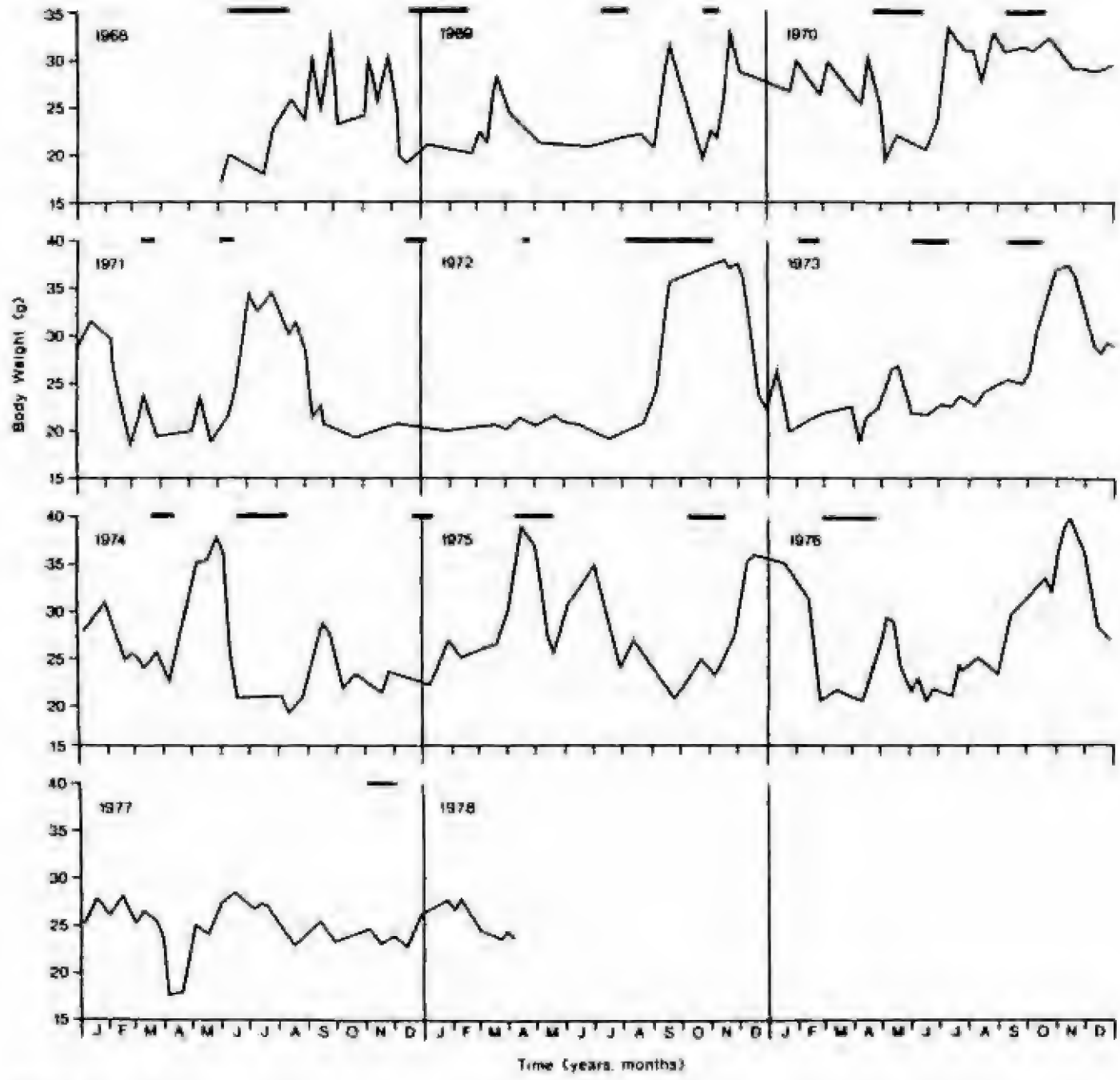

Figure 2

Body weight changes and molt (black bars) in an individual garden warbler, kept in constant conditions (daily dark:light ratio 10:14 hours) for a 10-year period. For details see Berthold (1978).

Circannual rhythms as releasers for both migratory activity and migratory disposition have been convincingly demonstrated in 11 avian species, in detail for eight *Sylvia* species, the willow warbler (*Phylloscopus trochilus*), the chaffinch (*Fringilla coelebs*), and the crossbill (*Loxia curvirostra*). The rhythms are not restricted to typical migrants but are also well expressed in less typical migrants as in partially migratory Mediterranean warblers or in the vagrant crossbill.

The observed circannual rhythms normally have period lengths of about ten months and thus run faster than the calendar year. This deviation, quite regularly observed in birds, means that synchronizing factors from the environment must be able to adjust the biological "circa-clocks" to the appropriate seasons. Photoperiod, the annual changes of day length, has recently been proven to be such a synchronizer, a so-called zeitgeber. In a beautiful set of experiments Gwinner (1977a) demonstrated

its importance in the starling (*Sturnus vulgaris*), and I was able to show that photoperiod synchronizes migratory events, i.e., the annual cycles of migratory restlessness in the garden and in the Sardinian warbler (*Sylvia melanocephala*). Details of the physiological mechanism of this synchronization are not known. For review and more details, see e.g., Gwinner (1981a,b), Berthold (1980, 1982).

Patterns of Migratory Disposition and Restlessness: Endogenous Control and Low Sensitivity to External Influences

It has been shown in the previous section that in a migratory species, circannual rhythms can initiate migratory disposition and activity. Possibly these rhythms do not only start these events but control their entire course and thus are also responsible for length and pattern of these processes.

When comparing different species of Old World warblers with respect to their migratory activity displayed in captivity, it is striking to observe the tremendous species differences. Thorough investigations have shown that the amount of migratory activity is greater in species that normally migrate farther. In thirteen different species and populations (Fig 3) we found a positive correlation between the amount of migratory activity and the distance covered during the first fall migration ($r = 0.8$, $p < 0.01$). The amount of migratory activity would appear to be endogenously organized on a species level.

In order to better understand the extent of environmental and endogenous control of these processes, we have also carried out a set of eight experiments in defined conditions on the garden warbler to test the environmental influences on seasonal changes in migratory activity and body weight which occur during the autumn migratory season. All data were obtained from groups of at least ten handraised individuals during their first fall migratory period, and all individuals investigated displayed migratory restlessness. The results are depicted schematically in Figure 4. Gwinner (1974) (Fig 4B) depressed restlessness almost completely by darkening during the night for a period of two months. Despite this treatment, the subsequent course of restlessness in the experimental group was parallel to that of the control group and proved to be uninfluenced by the previous treatment. In two other experiments, (Fig 4C and D), I reduced migratory fattening by temporary starvation. In the case of moderate starvation, (Fig 4C), there was no influence on the pattern of restlessness. Severe starvation to a greatly depressed body weight (Fig 4D) resulted in the cessation of restlessness. But again, the subsequent course of body weight as well as that of restlessness in the experimental group was congruent with the control group and appeared to be uninfluenced by this severe experimental treatment. When we prevented the birds from fattening at the beginning of the migratory period (Fig 4E), we obtained similar negative results. The same holds true for an experiment with simulated weather conditions (Fig 4F) in which restlessness was almost completely suppressed in the experimental group on 22 completely dark and rainy nights. With the exception of a tendency in the experimental group to have a somewhat lower

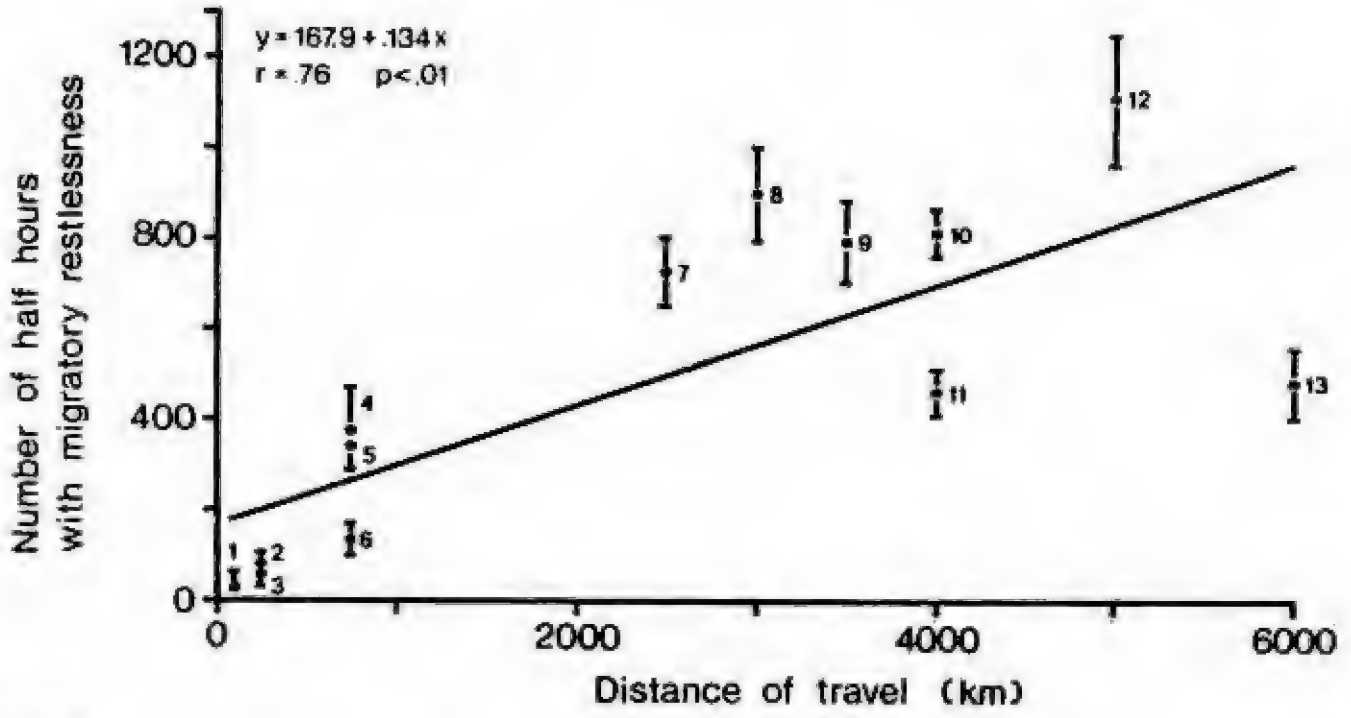

Figure 3

Relationship between the amount of migratory restlessness displayed in experimental groups and the distance covered in free-living conspecifics in 13 Warbler species and populations of the genus *Sylvia*. 1 = *S. conspicillata*, 2 = *S. sarda*, 3 = *S. atricapilla* (Canary Islands), 4 = *S. melanocephalata*, 5 = *S. undata*, 6–8 = *S. atricapilla* (S-France, S-Germany, S-Finland), 9 = *S. communis*, 10 = *S. cantillans*, 11 = *S. curruca*, 12 = *S. borin*, 13 = *S. nisoria*. From Berthold (1984).

overall restlessness and a slightly higher mean body weight, both groups showed congruent patterns of restlessness and body weight changes. When we handraised south Finnish birds (from 60°N) and south German birds (48°N) in simulated light conditions of their own breeding area or in those of the other population, all four groups of experimental birds showed almost identical patterns (Fig 4G). The only alterations of the endogenously controlled patterns of body weight and restlessness we ever found were observed when birds were kept in long-term constant, that is in unbiological, photoperiodic conditions. Then, as demonstrated in Figure 4H, birds kept in a light : dark ratio of 16:8 hours showed prolonged and flattened migratory patterns, and those kept in shorter days of 12:12 or 10:14 hours had short patterns compared with normal patterns obtained in simulated natural photoperiodic conditions. Also in a very recent experiment (unpublished) there were no detectable influences on the migratory patterns when conditions that birds would have to face when landing in the Sahara desert were simulated.

From this set of experiments (for review see Berthold 1984b) it seems that, at least in the garden warbler, the patterns of migratory disposition, expressed by increased body weight and of migratory restlessness are under extremely rigid endogenous control. Consequently, a direct and strict genetic basis appears most probable for the control of these patterns. According to these results the patterns are supposed to be innate and highly heritable, and a "sliding set-point" (reference signal, based on endogenous rhythms) in the sense of Mrosovsky and Powley (1977) is thought to determine the seasonally required values.

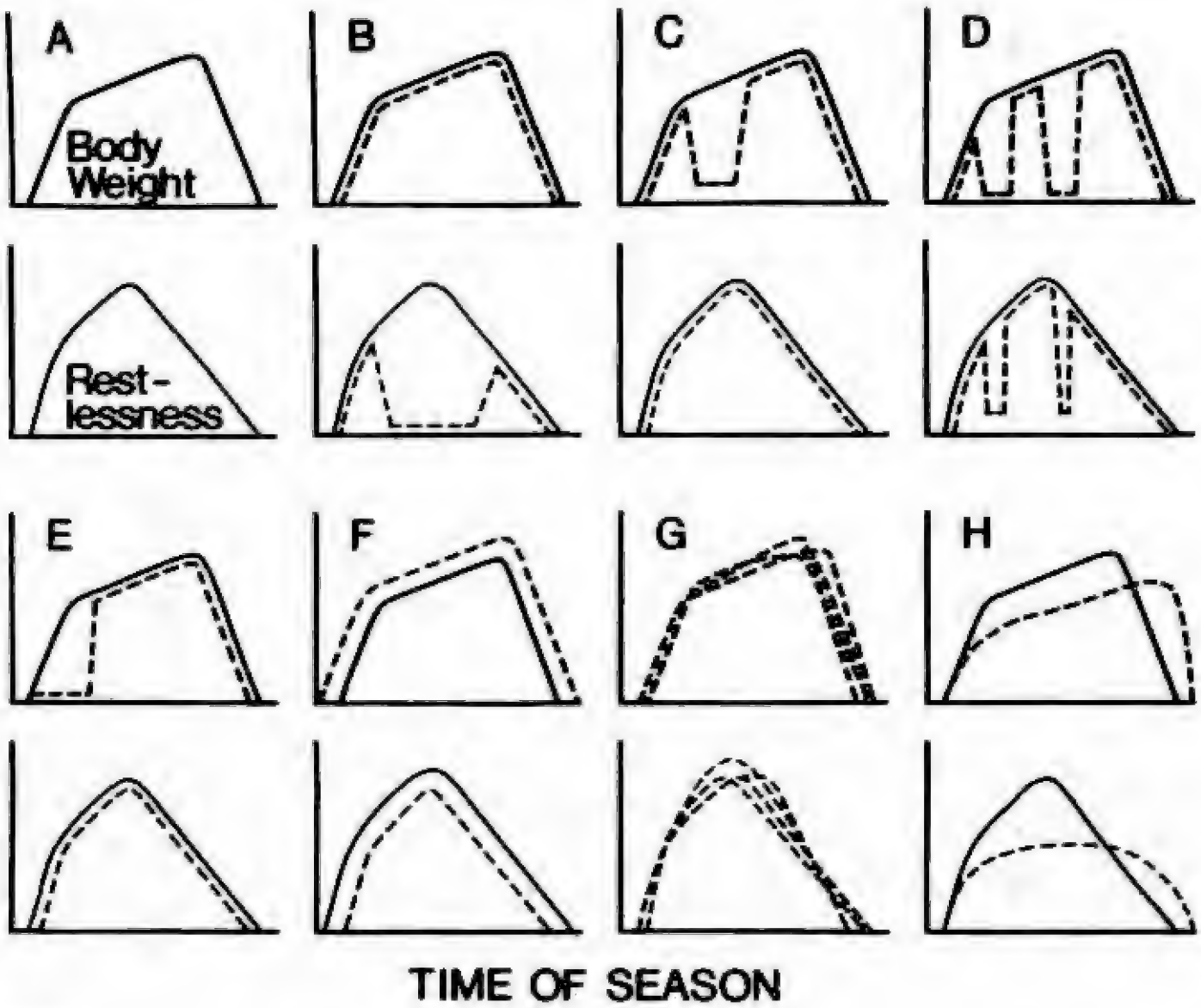

Figure 4

Schematic presentation of the normal course (A) of body weight changes (above) and of migratory restlessness (below) in *Sylvia borin*, and data from seven experiments (B−H) to test the effects of environmental influences on these patterns. Broken lines: data from experimental groups, solid lines: data from control groups. For details, see text, from Berthold (1984b).

Migratory Restlessness in the Blackcap: Genetic Control

Encouraged by the results obtained from the experiments summarized in the last section, we planned a long-term study with the aim of demonstrating the innate character in the amount and pattern of migratory activity by a cross-breeding experiment. For these experiments the blackcap (*Sylvia atricapilla*), a widespread species in Eurasia and northern Africa which has a strong geographical and ecological differentiation, appeared most suitable. We first considered whether populations of this species showed varying amounts of migratory restlessness in relation to the migratory distances as found in species comparisons (Fig 3). We handraised nestlings of three European blackcap populations and one African population. All birds were initially raised in identical, simulated natural light conditions. Their migratory restlessness was later measured in a light : dark ratio of 12.5:11.5 hours. The results

obtained (Fig 5A) are in accordance with the distances covered by the free-living populations from north to south. The degree of migratory restlessness was, as the patterns of restlessness show, greatest in the Finnish birds with progressively less in the German, French and African birds.

To demonstrate the innateness of migratory behavior with respect to amount and pattern, cross-breeding was considered the quickest and most promising method. If the expression of migratory activity were under direct genetic control, a polygenic control mechanism would be assumed. An intermediate expression of restlessness in both amount and pattern in hybrids from two parental populations that are differentiated by their restlessness would be expected. For our cross-breeding experiment we used the birds from which the data are presented in Figure 5A. For practical reasons we chose the African and German birds as parental stocks. We successfully handraised 32 hybrids in two years and used the same methods to record their migratory restlessness as had been used for their parents. As Figure 5B shows, amount as well as pattern of the restlessness of the F_1-hybrids are perfectly intermediate in comparison to their parental populations. Thus amount and pattern of migratory restlessness in the blackcap are shown to be under direct genetic control. With these findings in mind, it is no longer surprising that the pattern of restlessness in the even more typical migratory garden warbler proved highly insensitive to various environmental influences, as was shown above. For more details see Berthold and Querner (1981).

In this cross-breeding experiment we found similar results with respect to some morphological and physiological features strongly associated with migration such as body weight, wing length, and in the course of juvenile molt, all of which are important to the success of migration and to migratory performance. We found intermediacy in the F_1-hybrids in all of the above-listed traits (Berthold and Querner 1982a).

Migratory Restlessness: Possible Adaptive Value

When considering seasonal patterns of migratory activity in different species, marked differences become obvious not only with respect to the amounts of activity (Fig 3), but also with regard to their temporal distribution. Figure 6 gives an example. Species comparisons (as, e.g., in Fig 3) yielded the following characteristics: in long-distance migrants, normally crossing the Sahara desert, we regularly found fairly symmetric patterns with high central values, and these central values are in temporal accordance with the time of the Sahara crossing. Besides the garden warbler (broken line, Fig 6) we found patterns of this type in the subalpine warbler (*Sylvia cantillans*) and Orphean warbler (*S. hortensis*), in the whitethroat (*S. communis*) and in the nightingale (*Luscinia megarhynchos*) (Berthold 1973 and unpublished). In the barred warbler (*Sylvia nisoria*, solid line, Fig 6), which does not cross the Mediterranean and Sahara but travels from its middle- and SE-European breeding areas probably by flying completely around the Mediterranean by land to its east African winter quarters, we found a more flat pattern of restlessness which was

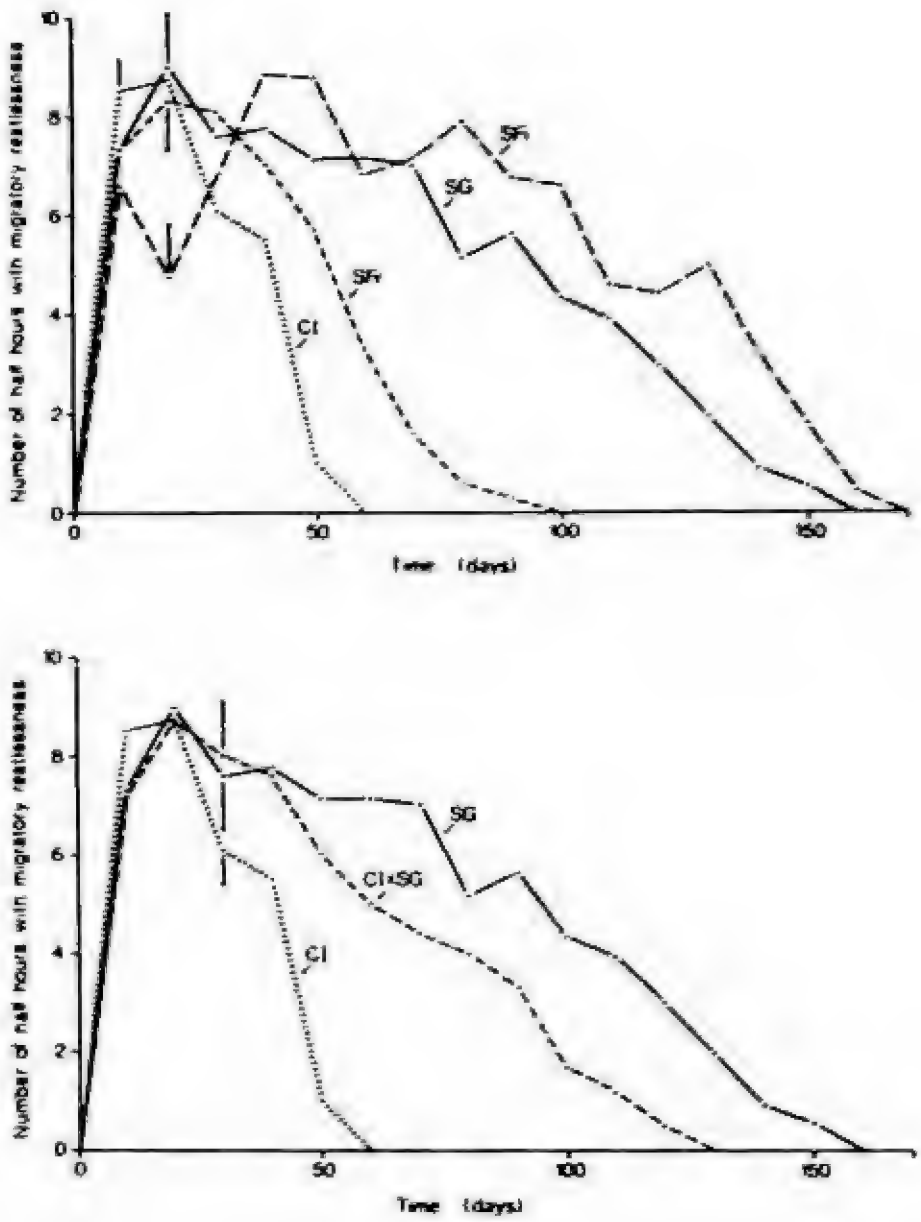

Figure 5

Time course of nocturnal migratory restlessness of groups of 24–32 blackcaps from three European and one African population (top) and from hybrids of two populations (bottom). Mean values for 10-day periods and some standard errors by way of example. SFi, birds from southern Finland, SG, southern Germany, SFr, southern France, CI, Africa, Canary Islands, CI × SG, hybrids. Berthold and Querner (1981).

somewhat skewed to the right. In the Mediterranean partial migrants, Marmora's (*Sylvia sarda*), Sardinian and Dartford warbler (*Sylvia melanocephala*, dotted line), we observed very flat patterns, and they were skewed to the left. The low overall restlessness and some peak activity towards the end of the migratory period are in full accordance with the course of migration in that group in which migratory individuals may leave the breeding grounds for some irregular movements during the summer but do not start their short-distance migration before late autumn (e.g., Blondel 1966).

According to the data presented, the patterns of migratory restlessness seem generally to express species-specific peculiarities of the migratory journey. With the genetic control of patterns such as these in mind, as has been demonstrated in the blackcap, it has to be suggested that these patterns possibly represent endogenous adaptations to the species-specific migratory journey.

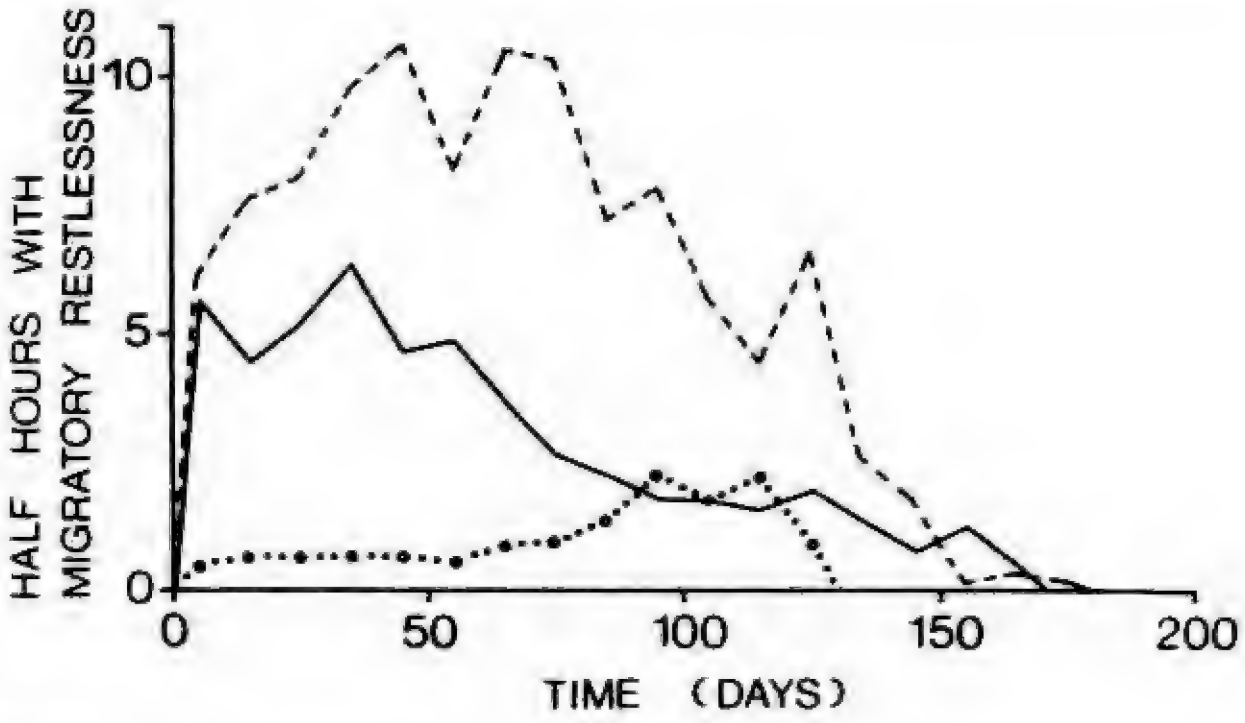

Figure 6

Patterns of migratory restlessness (mean values for 10-day periods) of groups of 6–10 individuals of three different warbler species. Broken line, garden warbler, solid line, barred warbler, dotted line, Sardinian warbler. From Berthold (1984).

In line with this hypothesis we have recently studied the marsh warbler (*Acrocephalus palustris*), stimulated by its unusual migration. According to several detailed studies, the marsh warbler leaves its European breeding grounds extremely early from mid-July onwards, crosses or surrounds the eastern Mediterranean and passes Ethiopia in east Africa about mid-August. Because it does not arrive before October in Kenya and not before late November in its winter quarters below central Tanzania, it has been suggested that the marsh warbler has a longer stopover period in Ethiopia, or that once having arrived in NE Africa, it could also move southwards steadily but much more slowly than before. In its southernmost winter quarters in South Africa it is not numerous before late December/January after a journey of about six months duration, but many birds may arrive even later. From our hypothesis we predict the following pattern of migratory restlessness: bipartite or to some extent biphasic, maximum values in the first part and of moderate size, and an extension of some six months. The experimental evidence from ten handraised S-German marsh warblers fits this assumption very well: we obtained a biphasic pattern of very long extension (Berthold and Leisler 1980). Thus patterns of restlessness investigated so far appear in fact as inherited anticipations of the migratory journey and as such are of extremely high adaptive value.

Innateness of Migratory Directions

As I have summarized in earlier papers (e.g., 1980), there is ample evidence from a number of experiments performed by several authors, that in about ten bird species the choice and/or maintenance of the species- or population-specific migratory direction has to be considered as inborn. The most impressive and convincing evidence was published by Gwinner and Wiltschko (1978) for S-German garden warblers. From the atlas of *Der Zug Europäischer Singvögel* (Zink 1973), it can be seen that central European garden warblers leave their breeding grounds initially in a southwesterly direction oriented towards the Iberian peninsula. All the winter quarters of the garden warbler in central and southern Africa are clearly south or even southeast of this intermediate goal. Thus a counterclockwise shift of the migratory direction roughly in the area of the Iberian peninsula has to be expected since no wintering on the South American continent is known in the garden warbler.

Gwinner and Wiltschko (1978) raised a total of 59 German garden warblers and kept them under constant temperature and photoperiod conditions throughout the fall migratory season. At regular intervals the birds were moved to circular orientation cages in which they were tested for directional preferences during their nocturnal migratory restlessness. It is evident from this experiment (Fig 7) that the caged birds prefered a more or less southwesterly direction during that time at which free-living garden warblers also fly in a southwesterly direction. The experimental birds then changed to S or SSE at about the time wild garden warblers perform a similar directional shift on the Iberian Peninsula or in northern Africa at the latest. The most parsimonious interpretation of these results would suggest that the changes in migratory direction occurring in this species are due, at least in part, to spontaneous endogenous changes in the preferred direction relative to external orienting cues. That is, directional preferences in this special case appear to be based on a counterclockwise endogenous "turn-table." Since the experimental birds were prevented from ever viewing the sky, Gwinner and Wiltschko (1978) believe the earth's magnetic field to be the most probable reference cue.

The Vector-Navigation Hypothesis

The results reported allow one to establish a comprehensive hypothesis for the control of avian migration. As shown, the available evidence favors the opinion that typical migratory behavior is based on a series of endogenous and heritable programs. In detail, the entire migratory behavior, at least in some species, appears to be related to a fundamental endogenous system—the circannual rhythms. These internal calendars initiate and terminate migratory events in connection with synchronizing factors, especially photoperiod. The pattern of migratory activity has to be considered as an inborn and heritable time-program for migration, programmed to species- and population-specific peculiarities of the migratory journey. The migratory direction can be, at least in a series of cases, understood in terms of an endogenously prescribed feature. Taking these findings together for many inexperienced migrants individually

Figure 7

Germany, during those periods at which freeliving conspecifics pass through certain banding stations (average passage dates in brackets). Hatched: winter quarters. From Gwinner and Wiltschko (1978).

migrating, it can be hypothesized that such birds should be capable of performing their first migratory journey by flying in their innately prescribed migratory directions just as long as their internal time-programs provide migratory activity. In this way they should "automatically" reach their hitherto unknown species- or even population-specific winter quarters. Migration thus appears to be performed along a vector which is composed of an inborn migratory route and a time-program indicating the length of that route. Fuel for migration seems generally to be provided in a similar way: again, an endogenous program creates a migratory disposition in which fat deposition is generated by hyperphagia. Body weight as well as migratory activity appear to be precisely controlled by special endogenous, sliding set-point mechanisms. For possible restrictions of the hypothesis see, e.g., Gwinner (1977b).

In this context it has to be emphasized that this vector-navigation hypothesis applies to inexperienced juveniles migrating for the first time. In elderly migrants, additional factors such as true navigation, learned environmental information and traditional use of breeding grounds, resting areas and winter quarters may well play an important role (for more details, see e.g., Schmidt-Koenig 1973).

Partial Migration: Innateness of the Migratory Urge and Polymorphism as a Controlling System

Partial migration, in my opinion, presents a unique opportunity to make progress in the study of many fields of bird migration. It can develop over a short period of time from exclusively migratory behavior, as, e.g., in the blackbird (***Turdus merula***), starling, or Canada goose (***Branta canadensis***). This provides a unique chance to conduct investigations of migratory and sedentary behavior in the status nascendi. I wonder if partial migration might not assume a key position in the study of the physiology and genetics of avian migration mainly because of excellent possibilities for (1) comparisons of closely related migrants and nonmigrants and (2) experimentation including cross- and selective breeding combined with subtle physiological investigations.

With respect to the control of partial migration in birds there are two controversial hypotheses. Mainly on the basis of ringing recoveries Lack (1943, 1944) proposed a genetic determination of migrants and residents that is a dimorphism. Kalela (1954) and recently Hildén (1982), on the other hand, hypothesized a behavioral-constitutional control mechanism with a facultative determination of migratory behavior. In Kalela's opinion, losers during autumnal territorial fights have to leave the breeding area as migrants, whereas winners can stay as residents (see Ketterson and Nolan, this volume for futher discussion of this point).

While investigating the migratory restlessness of Mediterranean warblers and blackcaps of European and African populations, we obtained from 1974 onwards the first experimental evidence for the control of partial migration in these species. The findings supported Lack's hypothesis: the development of restlessness in experimental groups in constant experimental conditions was a fairly good reflection of the different, that is typical and partially migratory habits, of the parent populations. Thus the different migratory habits seemed to be endogenously preprogrammed or innate. The next and more conclusive evidence resulted from a cross-breeding experiment between almost nonmigratory African and migratory German blackcaps. Here the percentage of birds displaying restlessness increased from 23 in the African parental generation to 56 in the F_1 offspring. The most plausible explanation for this finding is that an introduction of genes causing migratory restlessness from the German parents increased the proportion of migratory individuals in the F_1 hybrids or, in other words, that the migratory urge is innate and heritable.

In order to substantiate this explanation we started an experiment of selective breeding with southern French blackcaps in 1977. In a large sample of 102 experimental individuals from this population, known to be partially migratory, we found 77% migratory active and 23% migratory inactive birds. Assuming this migratory habit is based on polymorphism, selectively breeding the migrant and nonmigrant morphs should fulfill the following three predictions: (1) the offspring of migrants paired with migrants should show an increase in the ratio of migrants to nonmigrants compared with the original population and (2) compared with the offspring of nonmigrants paired with nonmigrants. Similarly (3) the offspring of pairing nonmigrants with nonmigrants should show an increased amount of nonmigrants compared to the original population. Up to 1981, we had successfully raised 39 birds of the F_1 generation and investigated their migratory activity in the same way as had been done earlier with the parental birds. Table 1 shows that the data obtained fulfilled two of the three predictions mentioned above: in comparison to the parental population, represented in the first row, the offspring of the nonmigrants, represented in the middle row, showed a significant (30%) increase in the number of nonmigrants. This ratio of nonmigrants to migrants was also significantly different from the offspring of migrants as the comparison with the data in the last row shows. Moreover, although not statistically significant, there was also some evidence in favor of the third prediction: the number of migrants in the offspring of migrants paired with migrants was 8% higher than in the parental population.

The results of this study demonstrate that in the partially migratory blackcap population, the characters "migratory" and "nonmigratory" are heritable and thus establish polymorphism as a controlling system of partial migration for the first time in birds (Berthold and Querner 1982b). They also confirm Lack's hypothesis from 1943/1944.

In the cross-breeding as well as in the selective breeding experiments, the alteration rate from one generation of birds to the next, i.e., from the parental to the F_1, was in our opinion surprisingly high with approximately 30% in both cases. If this speed of alteration endured during continued selective breeding, it has to be suggested that the partially migratory blackcap populations could become exclusively nonmigratory or migratory on a genetic basis after a few generations. Since selective breeding in captivity corresponds to high selection pressure in a wild population, our results imply a high evolutionary rate for partial migration in the blackcap when strong and directed selection pressures exist. They also show that partial migration can be a highly sensitive and reactive system to any sort of environmental factors influencing fitness in the breeding grounds, in the winter quarters, and during migration. The diphenism of partial migration hence appears to be a genetic dimorphism, and the strategy of maintaining both a migratory and a nonmigratory portion of the population seems to be controlled quantitatively by a highly sensitive balanced polymorphism integrating any environmental influences from the year round living area (discussed in detail, e.g., by Gauthreaux 1980).

Table 1

Proportions of migratory active and inactive blackcaps in the original southern French population and in selectively bred F_1 generations. From Berthold and Querner 1982b.

	Original French Population $n = 102$		F_1 Nonmigrants × Nonmigrants $n = 19$		F_1 Migrants × Migrants $n = 20$	
Number of Migrants	79	(77%)	9	(47%)	17	85%
Number of Nonmigrants	23	(23%)	10	(53%)	3	(15%)
				$p < 0.01$		$p < 0.025$

In the meantime, H. Schwabl and H. Biebach in our institute have investigated partial migration in the blackbird and in the robin (*Erithacus rubecula*). Schwabl raised nestlings from parents known to be nonmigrants from ringing and subsequent observation, and from obvious migrants. He then tested their migratory behavior in the laboratory. Biebach conducted a selective breeding experiment comparable to ours reported for the blackcap (for review see Berthold, in press). From both studies there is similar experimental evidence for the innateness of the migratory urge in these partially migratory species as in the blackcap. There are also corresponding findings from field data in the stonechat (*Saxicola torquata*) by Dhondt (1983). Thus polymorphism as a controlling system of partial migration seems possibly to be common in birds and may allow further studies on the basis of a wider scale of species.

Habitat Preferences in Migrants: Preprogrammed Choice

Migrants traveling across country are regularly faced with more or less new patterns of different (micro)habitats when they stop in an appropriate resting area. This resting area should be chosen as quickly and efficiently as possible in order to allow for resting, fuel replenishment, seeking shelter, etc. In a long-term ten-year trapping program we have studied how passage migrants do this. Analyzing the data from the first five years of this program of about 70,000 trapped individuals of about 40 species of mainly songbirds at three trapping sites in central Europe, we found the following: trapping was characterized by clearcut species-specific "trapping figures," which, according to additional investigations, proved to express the habitat preferences. Figure 8 shows that most of the lesser whitethroats were caught in two small sectors. Furthermore, these figures and thus the underlying habitat preferences

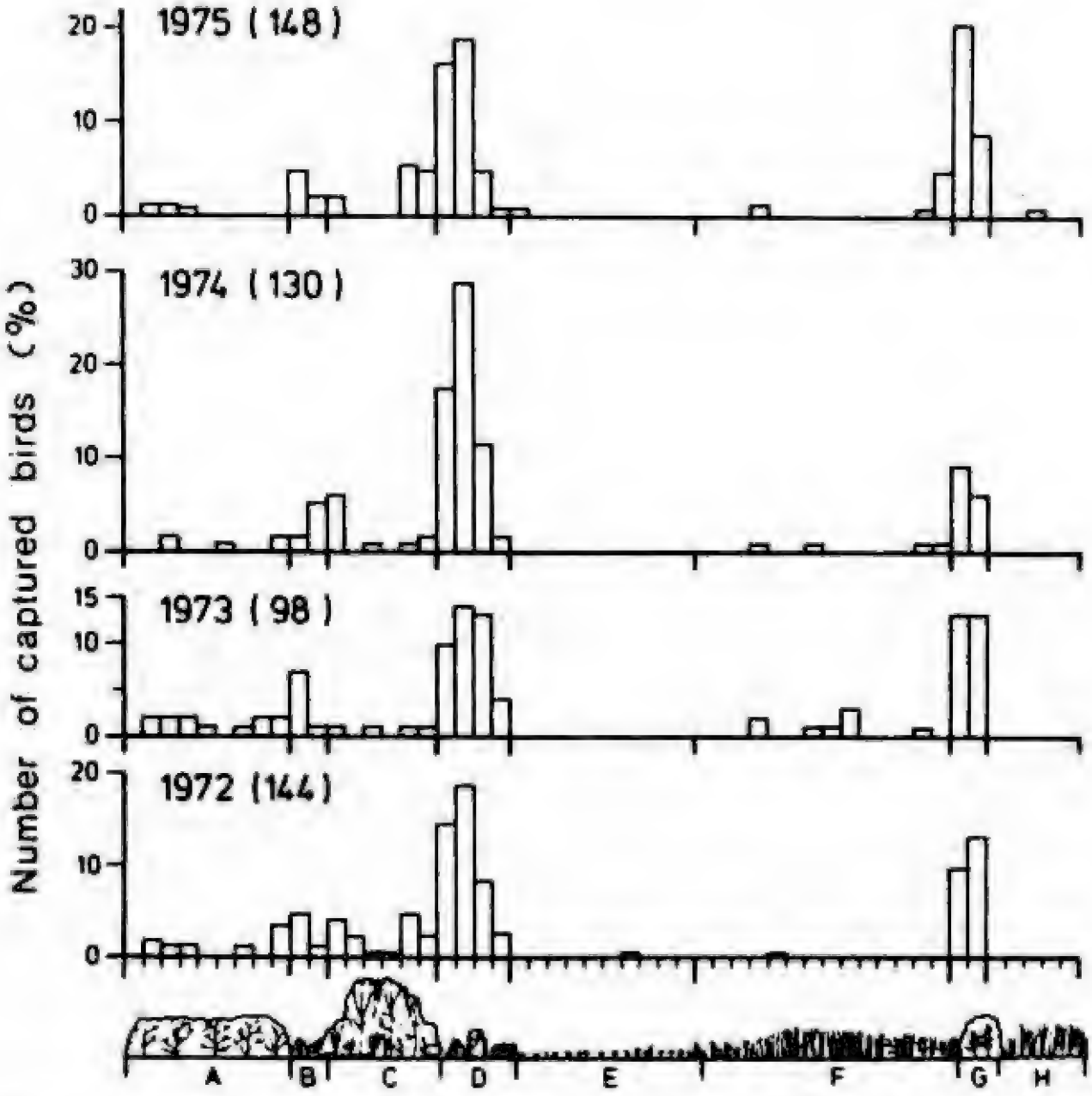

Figure 8

Distribution of trapped lesser whitethroat *Sylvia curruca* caught during the autumn migratory period in 52 mist nets set up in 8 different habitats (A−H) in 4 consecutive years in a resting area in south Germany. From Bairlein (1981).

were amazingly constant from year to year.

Using cluster analysis and principal component analysis, my coworker Bairlein (1981) found that these habitat preferences are primarily related to characteristic morphological prerequisites, above all to those of the flying apparatus. Comparisons of the habitat preferences of juveniles and adults indicated that the choice of these species-specific habitats is largely innate and is only little if at all improved or altered by learning. Thus passage migrants appear to be equipped with some type of inherited habitat conceptions (i.e., innate ideas of the appropriate habitats) which produce very clearcut species-specific habitat preferences even in hitherto unknown resting areas. It is suggested that these preferences are accomplished by visual inspection while airborn and during landing. This endogenously controlled system of habitat preferences should provide avoidance of interspecific competition during migration and optimum resource utilization until geographical regions with other competitive bird communities are reached. According to these findings, even such a

relatively simple behavioral trait of a migrant as the spontaneous daily choice of a suitable resting area is deeply anchored in the bird's behavioral physiology.

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ONTOGENY OF MIGRATORY ORIENTATION: A LOOK AT THE PIED FLYCATCHER, *FICEDULA HYPOLEUCA*

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ABSTRACT

The pied flycatcher ***Ficedula hypoleuca*** is a European-trans-Saharan nocturnal migrant whose orientation behavior has been intensively studied. In this paper, we review our current knowledge of the ontogeny of migratory orientation in this species. The experiments we describe all involved manipulating the exposure of hand-reared pied flycatchers to known sources of directional information (i.e., the geomagnetic field, the night sky and the setting sun) either during the birds' first summer and/or during the time of their first autumn orientation tests. Collectively, the results emphasize the complexity of a young pied flycatcher's developing orientation system that includes both orientation responses to environmental stimuli which develop independently of experience with other directional cues and those which can be modified as a result of experience with other cues.

INTRODUCTION

Recent advances in our understanding of how animals organize their movements in space have resulted in a review article on the general mechanisms of animal orientation and navigation (Able 1980). Regarding birds, review articles have also appeared on compass mechanisms (W. Wiltschko 1983) and the ontogeny of homing behavior in pigeons (R. Wiltschko 1983). But despite the considerable progress made in revealing the complexities associated with the ontogeny of the orientation behavior of migratory birds, a synthesis of this work has yet to appear. Instead of a general survey of this phenomenon, however, we have chosen to focus our review on that species which has been most intensively studied in our laboratory: the pied flycatcher (***Ficedula hypoleuca***).

As in any ontogenetic analysis, an understanding of the mature behavioral form, whether it be fixed or still changeable, is necessary. For this purpose we will assume, as has been shown for other nocturnal migrants (cf., W. Wiltschko 1983), that as adults, pied flycatchers can use the geomagnetic field, stars and cues associated with

the setting sun (either the setting sun itself (Moore 1982) and/or skylight polarization associated with it (Able 1982) as ***independent orientation cues*** in locating their migratory direction. By independent, we mean that a bird can use the environmental stimulus in question to display an orientation response for migration in the absence of any other sources of known, relevant directional information. With the cautionary note that adult pied flycatchers have only been examined for their ability to orient by the earth's magnetic field during migration (Beck and Wiltschko 1981), the questions we will examine are: (1) what are the experimental prerequisites needed by a young bird to develop an independent migratory orientation response to each of the previously mentioned environmental stimuli, and (2) to what extent can the formation of an orientation response to one cue be influenced through experience with another source of directional information. At this point, we should emphasize that the experiments we will discuss all involved hand-reared, captive birds, and used various cage devices to determine their directional preferences (see Beck and Wiltschko 1982 for a methodical description). The statistics applied are described by Batschelet (1981).

EARTH'S MAGNETIC FIELD

In experiments designed to examine the ability of naive migratory pied flycatchers to display migratory orientation with respect to an ambient magnetic field, Beck and Wiltschko (1982) took nestling pied flycatchers and hand-reared them in a windowless laboratory. During the course of the summer and the autumn testing season the birds were held indoors and were thus deprived of any opportunity to view the sky and the orientation cues associated with it. At the beginning of the migration season, middle August, the birds were placed in orientation cages located indoors, and their nocturnal activity (zugunruhe) was recorded. Figure 1 gives the orientation of these birds when tested in the local geomagnetic field and in an experimental magnetic field with magnetic north shifted 180° relative to the earth's local field. The data show that without ever viewing the sky, naive migratory pied flycatchers were able to use an ambient magnetic field to display migratory orientation as had been demonstrated previously for garden warblers (*Sylvia borin*, Wiltschko and Gwinner 1974) and savannah sparrows (*Passerculus sandwichensis*, Bingman 1981a).

Pied flycatchers, like many western European trans-Saharan migrants, are confronted with a variety of en route topographical barriers (e.g., the Alps, the Mediterranean Sea and the Sahara Desert) during migration. It is presumed that these barriers play some causal role in the southwesterly movement through Europe and the subsequent south–southeasterly movement to central Africa which characterizes their autumn migration. Figure 2 gives the magnetic field orientation of a group of hand-reared pied flycatchers kept and tested without their ever having seen the sky. The data are divided into the early and late stages of migration (Beck 1984). As can be seen, the test birds displayed a seasonal shift in their orientation which corresponded nicely to the shift in migratory direction presumed to occur in free-flying conspecifics. Similar findings have been obtained by Gwinner and Wiltschko (1978) using hand-

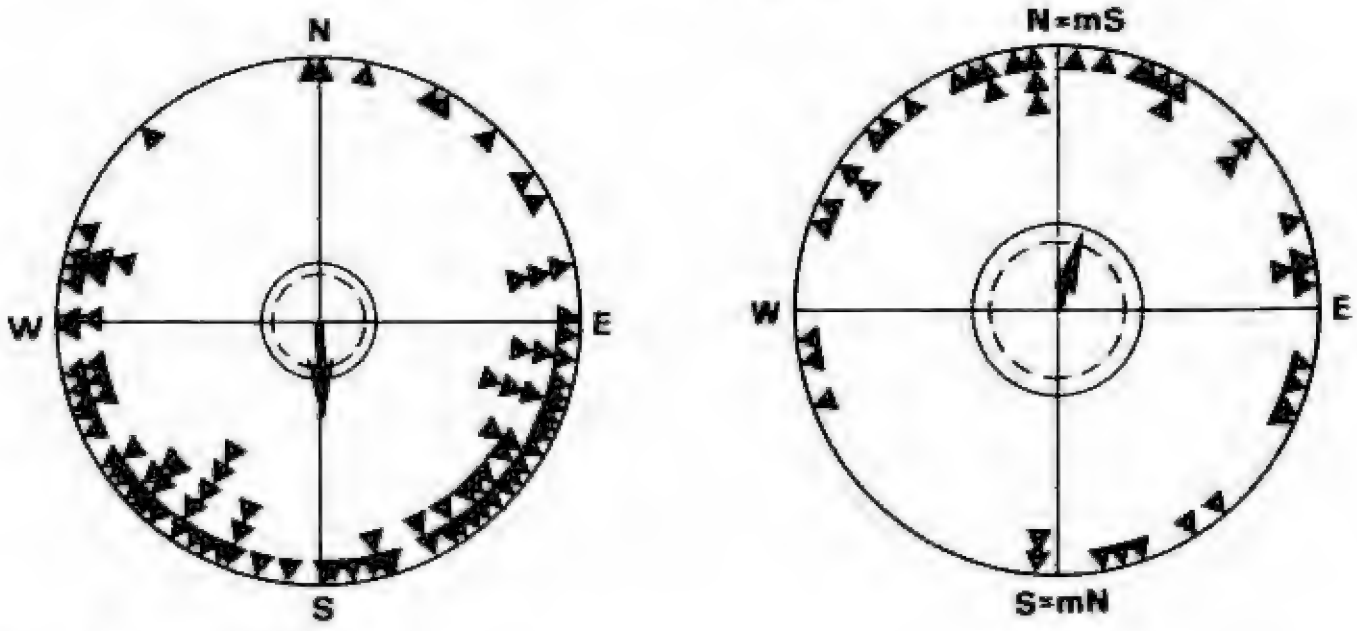

Figure 1

First autumn orientation of hand-reared pied flycatchers prevented from ever viewing the sky and tested without celestial cues. (a) Tests in the local geomagnetic field (b) Tests in a magnetic field shifted 180° relative to the local geomagnetic field (data from Beck and Wiltschko 1982). The triangles at the periphery of a circle represent the mean headings of individuals for each period tested. The mean vector is shown as an arrow, its length drawn proportional to the radius of the circle = 1. The two inner circles represent the 5% (dotted) and 1% significance levels of the Rayleigh test.

reared garden warblers. In contrast to garden warblers, however, pied flycatchers showed a shift in direction only if they experienced a change in magnetic intensity and inclination which simulated the magnetic field conditions which migrants experience when they reach southwestern Europe. When continually tested in a magnetic field simulating central Europe, the birds became disoriented in the latter part of the season (Beck 1984). Based on these results, it would appear that directional information from the geomagnetic field alone is sufficient to allow young pied flycatchers to reach their wintering quarters. They not only can take up an initial course by referring to the magnetic field, but they can display an appropriate shift in this orientation as well. The data are consistent with the hypothesis of a preprogrammed route to central Africa based on vector navigation (see Berthold 1984 and this volume).

Unfortunately, the possible importance of exposure to a magnetic field for the maturation of a migratory response to the geomagnetic field remains unknown. In one relevant experiment (Alerstam and Högstedt 1983), pied flycatchers were exposed to an altered magnetic field during the egg and nestling stage. In the following autumn migration season, differences were found between the orientation of these birds and that of untreated controls. It is not clear, however, whether the differences were caused by an altered reaction to the magnetic field or whether other factors which were also present during the tests were involved (see below).

Remaining to be answered, however, is whether the development of a young bird's orientation response to an ambient magnetic field can be influenced by experience with other sources of directional information. A first indication that such an effect exists came from experiments which showed that if hand-reared garden warblers were able to view the sky during the time of their first summer, their magnetic field orientation during autumn migration was worse than that of hand-reared birds that had never seen the sky (Wiltschko, Gwinner and Wiltschko 1980). Later,

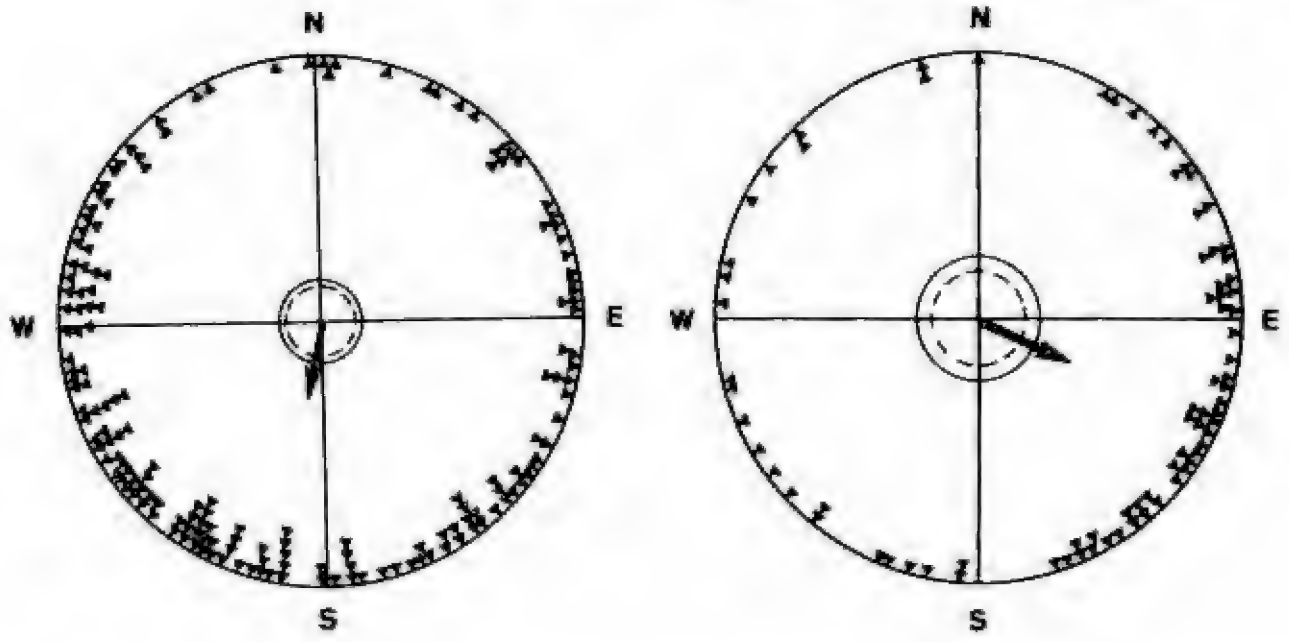

Figure 2

First autumn orientation of hand-reared pied flycatchers prevented from ever seeing the sky. The birds were kept and tested in magnetic fields simulating those experienced by free-flying conspecifics during migration. (a) Early part of migration, 29 Aug−14 Oct. (b) Later part of migration, 15 Oct−12 Nov. (Data from Beck 1984.) Symbols as in Figure 1.

Bingman (1983a) observed that hand-reared savannah sparrows which spent their first summer in conditions that varied the relationship between an ambient magnetic field and geographic north showed different directional tendencies when tested in the earth's local magnetic field in the absence of visual cues in autumn. In fact, the orientation of the birds differed in a manner consistent with the hypothesis that savannah sparrows are able to modify their response to the magnetic field experienced during their first summer in order to maintain orientation in a fixed geographic direction.

The extent to which first summer experience with the sky can influence the magnetic field orientation of pied flycatchers was studied by hand-rearing two groups of birds. After fledging, they were housed outdoors and given full day and night exposure to the natural sky. The controls lived in the local geomagnetic field, while the experimental group was exposed to a magnetic field which was shifted ca. 115° counterclockwise (magnetic total intensity and inclination were approximately the same as the local geomagnetic field). The orientation of both groups during autumn migration in the earth's local magnetic field without view to the sky is plotted in Figure 3. The birds that were raised in the earth's local field displayed seasonally appropriate, southerly orientation, while the birds raised in the shifted field, showed considerably poorer orientation and preferred a north−northwesterly direction. With respect to their rearing treatment, the experimentals' preference of magnetic NNW would have corresponded to geographic E, so that the effect of rearing the birds in an altered magnetic field is not easily interpreted. More data will be necessary to find out whether the migratory direction with respect to the ambient magnetic field can be modified by early sky experience, as Bingman (1983a) suggested.

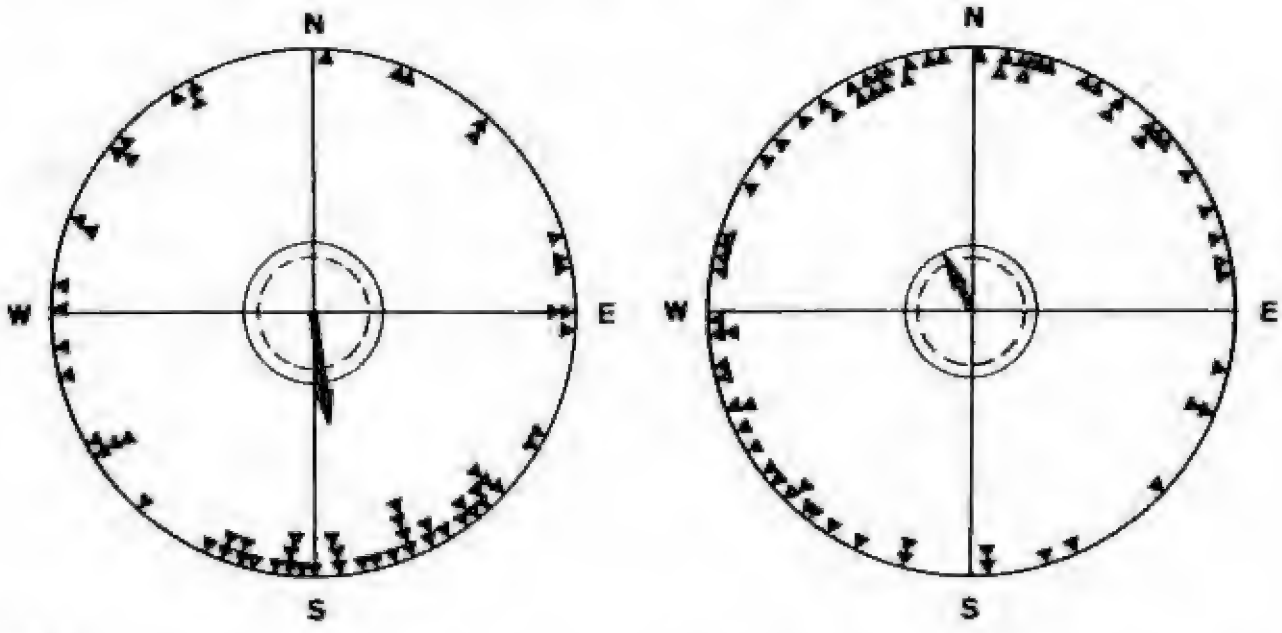

Figure 3

First autumn orientation of hand-reared pied flycatchers kept outdoors during the summer with a full view to the sky. The birds were tested in the *local geomagnetic field* without celestial cues. (left) Birds that spent the summer in the local geomagnetic field. (right) Birds that spent the summer in a magnetic field shifted by ca. 115° counterclockwise relative to the local geomagnetic field. (Data from Bingman, in preparation.) Symbols as in Figure 1.

STARS AND NIGHT SKY

The first experiments examining the role of stars in the orientation of nocturnal migrants were performed by Sauer (1957). His results led him to the conclusion that European warblers (gen. *Sylvia*) possess an experience-independent star compass. A series of experiments by Emlen (1969, 1972), however, contradicted this assumption. Emlen's findings emphasized the important role of experience in the formation of a bird's star compass. He showed that it was the rotation of the night sky around its axis which acted as a reference for the formation of the star compass that would be used by young indigo buntings (*Passerina cyanea*) during their first migration. Examining the development of stellar orientation in garden warblers, Wiltschko (1982) obtained results suggesting that the rotational axis of an artificial night sky was more important for the formation of a star compass than the ambient magnetic field experienced by the birds during their first summer.

It is not yet known how young pied flycatchers form their star compass, but that they have a star compass, or more properly, a night sky compass, at the time of first migration was demonstrated by Bingman (1984). This study, however, focused on the question of whether the ambient magnetic field experienced during the first summer functioned as a calibrating reference in the setting of a young pied flycatcher's migratory orientation response to the night sky. To test this, three groups of birds were hand-reared and then transferred outdoors where they were housed for the summer in full view of the natural day and night sky. The control group was kept in the local magnetic field, a second group was exposed to a magnetic field the north of which was turned by ca. 105° to geographic WSW (total intensity and inclination were about the same as in the local magnetic field), and for the third group, the magnetic field was partly compensated so that the inclination was vertical, and the birds could

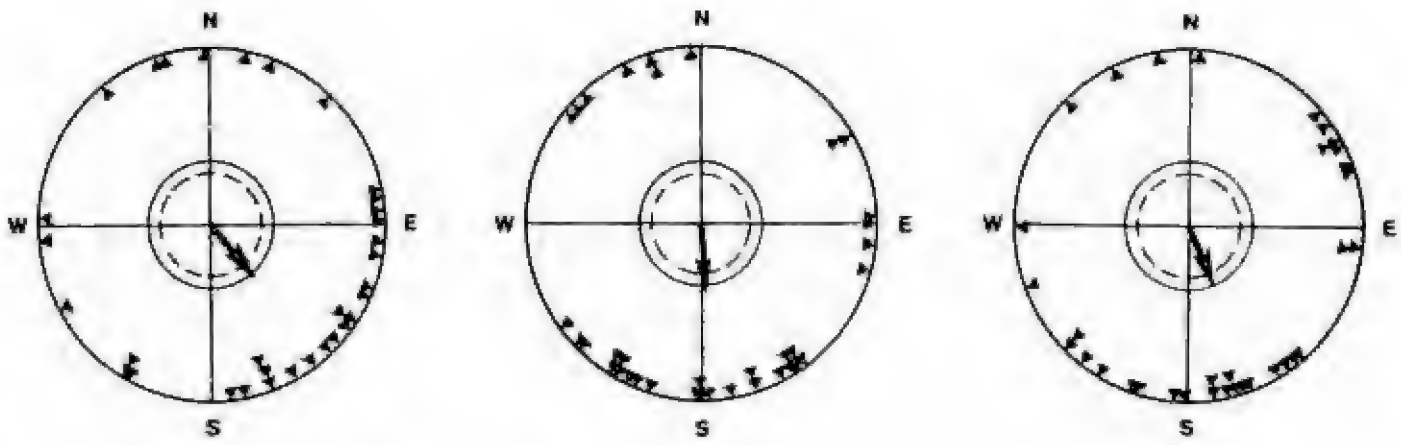

Figure 4

First autumn orientation of hand-reared pied flycatchers kept outdoors during the summer with a full view to the sky. The birds were tested under the natural night sky in a vertical magnetic field. (Left) Birds that spent the summer in the local geomagnetic field. (Center) Birds that spent the summer in a magnetic field shifted by ca. 105° counterclockwise relative to the local geomagnetic field. (Right) Birds that spent the summer in a vertical magnetic field. (Data from Bingman 1984.) Symbols as in Figure 1.

not derive any meaningful directional information from it. Figure 4 shows the autumn orientation behavior of all three groups when tested under the night sky in a vertical and thus meaningless magnetic field. Although the orientation of the three groups differed slightly, differences of the expected magnitude and direction consistent with the hypothesis of a magnetically based star compass failed to emerge. Thus the results lend no support to the hypothesis that the magnetic field serves as a calibrating reference in the formation of the pied flycatcher's initial night sky orientation response for migration. Similar results were also obtained by Rabøl and Dabelsteen (1983) who recorded southerly, night sky migratory orientation from hand-reared pied flycatchers that were continually exposed to an aberrant magnetic field of large vertical intensity. Results from hand-reared savannah sparrows (Bingman 1981b) also showed no difference in the night sky orientation of birds raised outdoors in different magnetic fields. Taken together, the results suggest that the development of a young bird's initial migratory orientation response to the night sky is independent of the bird's previous magnetic field experience. It seems to depend on celestial rotation and the directional information derived from it. As a directional stimulus, the rotation of the night sky represents a temporally and spatially stable indicator of geographic north. These characteristics would also qualify it as a possible geographic reference which could be used by young migrants to redefine their response to the geomagnetic field, as suggested by the findings of Bingman (1983a).

There is evidence, however, that during actual migration, experienced birds (including first year migrants captured during migration) rely on the earth's magnetic field as their primary source of directional information. In fact, they can use an ambient magnetic field to modify their stellar orientation (Wiltschko and Wiltschko 1975a,b). Although the pied flycatcher was not among the species tested, these findings seem to run contrary to the results presented above. A possible explanation

might be based on the fact that the rotation of the night sky plays a crucial role as a source of directional information only during a sensitive period during a bird's first summer and loses its importance with the onset of migration (Emlen 1969, 1972). After that, a bird's star compass, originally calibrated from the rotation of the night sky, could be influenced by the magnetic field.

SETTING SUN AND CUES ASSOCIATED WITH IT

It is in discussing sunset orientation that we are most restricted by a relative paucity of data. Young savannah sparrows, however, were shown to be unable to orient at sunset in the absence of meaningful magnetic field information (a vertical field) during the time of their first migration (Bingman 1983b) despite the ability of adult birds to use the setting sun as an independent orientation cue for migration (Moore 1982).

Regarding pied flycatchers, Alerstam and Högstedt (1983) recorded the sunset orientation of hand-reared birds in the presence of the local geomagnetic field during autumn migration. They tested three groups of birds that had experienced different magnetic fields as nestlings, and their findings were consistent with the hypothesis that the young birds had calibrated a secondary cue, presumably a cue associated with the setting sun, from the different ambient magnetic fields experienced as nestlings, and used it during the orientation tests. Present information from the geomagnetic field was thought to be ignored. If their interpretation is correct, it would lend further support to the idea that orientation by the setting sun, by whatever means, is first dependent on a calibrating reference defined by the earth's magnetic field. The difference between savannah sparrows and pied flycatchers might then only be a matter of the timing of the calibration process. Of further interest is that these results are in agreement with those obtained when the development of sun orientation in homing pigeons was studied (Wiltschko, Wiltschko, Keeton and Madden 1983).

SUMMARY

Young pied flycatchers (***Ficedula hypoleuca***) are able to use either the earth's magnetic field or the night sky as primary sources of directional information for migration. Both systems can develop independently of each other; i.e., a functional response to the magnetic field is found in birds that never saw the sky, and a functional response to the night sky is found in birds independently of their previous magnetic experience. The amount of experience with an ambient magnetic field or the night sky needed by a young bird for the proper development of its migratory orientation responses to these cues remains unknown. Likewise, it is not clear whether the directional relationship between the night sky and the ambient magnetic field during first summer has an effect on the direction selected with respect to the magnetic field during autumn migration. Directional cues associated with the setting sun do not seem to have directional significance by themselves. Existing data seem to suggest that the pied flycatchers' response to such stimuli is dependent on a reference

defined by an ambient magnetic field.

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INTRASPECIFIC VARIATION IN AVIAN MIGRATION: EVOLUTIONARY AND REGULATORY ASPECTS

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ABSTRACT

When some classes of a bird population migrate and others do not, or when classes migrate varying distances, survivorship during the non-breeding season is likely to differ among the classes because they spend that season in different environments. Knowledge of relationships among seasonal mortality rates, annual mortality rates, and productivity of migratory classes contributes to understanding of the advantages and disadvantages of migration and of the maintenance of the behavioral differences in the populations studied. At the proximate level, investigation of intrageneric and intraspecific variation in migratory behavior has been and continues to be important for elucidating mechanisms that regulate migration.

We have studied migratory dark-eyed juncos (***Junco hyemalis hyemalis***), in which females migrate farther southward into the winter range than males and adults farther southward than young of the year. These differences in winter distribution result in geographic variation in winter mortality of the sex-age classes, but evidently not in differences in annual mortality. We summarize the population dynamics by which we believe the winter distribution is maintained year after year and the ultimate factors that may select for the interclass differences. We also report results of an experiment in which the autumn and spring zugunruhe (nocturnal restlessness) of members of the four classes, all from a single breeding locality, was monitored. We asked whether quantitative differences in restlessness existed among sex-age classes and, if so, whether these correlated with the observed differences in distance migrated. Classes making longer migrations did tend to be more restless, but in most comparisons not significantly so. If zugunruhe reflects a physiological disposition to migrate whose duration and intensity have an underlying genetic basis, we conclude for the junco that conditions experienced in transit probably modify this disposition and therefore play an important role in determining average distance migrated by the sex-age classes.

INTRODUCTION

The existence of variation in migratory behavior among members of the same species provides unusual opportunities for probing both ultimate and proximate factors underlying migration (Myers, Maron and Sallaberry 1985). Among avian migrants, three types of intraspecific variation have been described.

1. In some species there are migratory and non-migratory populations; all individuals migrate from some regions of the breeding range, but all are sedentary in others.
2. In partially migratory populations, a portion of the individuals from a given population migrates, while the other portion remains sedentary.
3. Finally, in differential migrants all individuals migrate, but they differ predictably from one another in distance traveled (or, some would add, in direction and/or timing of movement; Gauthreaux 1982). All types of variation can occur within a single species. For example, high-latitude breeding populations may be entirely but differentially migratory, middle-latitude populations partially migratory, and low-latitude populations resident, as seems to be the case with ***Sylvia atricapilla*** (Mead 1983, p. 57).

In birds the intraspecific migratory differences that have been most often described (Gauthreaux 1982, Ketterson and Nolan 1976, 1983a) are associated with sex and/or age. When the difference is sexual, males are more likely than females to be the resident class or the class that migrates the shorter distance. When age bias occurs, the pattern is less clear. In partial migrants the tendency to migrate usually decreases with age, but in differential migrants, adults may travel either longer or shorter distances than young (in addition to citations in Gauthreaux 1982, see Spaans 1977, Ketterson and Nolan 1983a, p. 366, Morton 1984). Whether predictable variation also occurs commonly among members of a single sex-age class is not known. Across-class differences in migratory tendency can be relatively easily identified by studies at the population level, i.e., either (1) by detecting at one or more points in the winter range, deviations from the expected sex or age ratio of the population as a whole or (2) by observing variation among ratios in different parts of the range. On the other hand, determination that differential migration occurs within a single sex-age class usually (but not invariably) requires knowledge of the breeding and non-breeding locations of specific, marked individuals of that class, and information of this kind is scanty.

In this paper we first review hypotheses that have been advanced to account for the long-term maintenance of intrapopulation differences in distance migrated, i.e., to explain why selection has not eliminated the variation. We then focus on the differentially migratory population of the dark-eyed junco (***Junco h. hyemalis***), a bunting of the north-temperate zone. Our purposes are (1) to summarize the geographic variation in the junco's winter population structure, which we view as the product of a differential autumn migration; (2) to consider the population dynamics that maintain the geographic differences over the years; (3) to describe ultimate factors

that we believe underlie differences in distance migrated; and (4) to present results of an experiment investigating physiological mechanisms that may regulate the variation in the junco's migratory behavior. Data on points (1), (2) and (3) are summarized from work already published (Ketterson and Nolan 1976, 1982, 1983a); data on point (4) appear for the first time.

EVOLUTION AND MAINTENANCE OF INTRASPECIFIC VARIATION IN MIGRATORY BEHAVIOR

General Hypotheses

If all members of a species are migratory because the probable benefits of seasonal movement exceed (or, historically, exceeded) the probable benefits of remaining sedentary, then it follows that when only certain individuals migrate (or migrate farther), for them the advantages of migration (or prolonged migration) should outweigh the advantages of remaining sedentary. For their non-migratory or less migratory conspecifics the reverse should be true. These generalizations are, of course, idealized. Environments change, phylogenetic constraints limit the precision of selection, and chance may play a powerful role. Further, the individual is probably rarely in a position (or physiological state) that lets it first assess the full range of options available and then adopt the optimal course of behavior. Still, we would argue that assumptions of the general efficiency of selection and of the malleability of migratory behavior may be more justified when applied to the migrations of birds than to those of animals that are less mobile. Many birds, because they can cover long distances at high speed, are exposed within a single lifetime to a wide choice of environments in which to settle. It seems likely that each generation gives rise to some individuals that lack the mechanisms responsible for departing on the population's usual schedule, or for departing at all, others that settle between the normal breeding and wintering ranges, and still others that move entirely beyond the limits of one or both ranges. (Thus in a sample of migratory prairie warblers ***Dendroica discolor*** found outside the winter range of the species, all that could be aged were young individuals that were making or had just made the first migration of life (Nolan 1978, pp. 449–451; see also De Sante 1983).) If any of these deviations in migratory behavior were genetically based, and if it improved reproductive success, it would appear that in birds, unusually favorable and frequent opportunities exist for selection to increase the frequency of such variants (see Berthold and Querner 1982, Berthold, this volume).

When variation in the migratory behavior of a bird population is assumed to be stable over time, questions like the following arise: Do migrants and non-migrants, or long- and short-distance migrants, whatever their genetic distinctness, represent equally adaptive alternative strategies? If so, is that because environmental variation and unpredictability makes neither alternative consistently more advantageous than the other, or would the variation persist in the absence of environmental differences from year to year? Can alternatives be maintained even if they are not equally adaptive?

Various authors have addressed these problems and proposed models designed to answer one or more of them. We summarize these here but note in advance that data, particularly demographic and population-genetic data, are too scanty to test them in most cases (Myers et al. 1985).

Two hypotheses (Lack 1954, p. 224, 1968, von Haartman 1968)—both advanced to explain how a sedentary element and a migratory element can persist indefinitely and thus maintain a partially migratory population—assume that the elements are genetically differentiated forms. Although von Haartman (1968, p. 1) did not emphasize this, it is clear that his model requires a genotypic difference. Both authors also assumed that fitness of the migrant and non-migrant morphs must be equal over the long term or one would be eliminated. The equality must derive from some combination of compensatory trade-offs in (1) probability of surviving to adulthood, (2) annual productivity, and (3) annual survivorship while reproductive. Lack focused on survivorship alone and on the unpredictability of temperate-zone winters: more migratory individuals survive in years of unusual severity; in moderate winters mortality associated with migration exceeds the mortality of sedentary individuals. Over the years, annual survivorship balances out. Von Haartman proposed no equality of survivorship. In his view, non-migrants might always suffer greater winter (and therefore annual) mortality; but if competition for breeding resources was intense and sedentary individuals were more successful competitors, their greater productivity might compensate for their higher mortality. Thus, for cavity-nesting birds, nest sites may be limiting, and year-round residency may confer priority of access to these (Lundberg 1979).

More recently, Greenberg (1980) extended and modified von Haartman's argument, noting that among new-world passerines higher annual survivorship and lower productivity are associated with longer migrations; long-distance migrants live longer but produce fewer young per breeding season (Table 1). In Greenberg's view, however, greater productivity of sedentary species and short-distance migrants does not stem from prior access to resources. Rather, such species have more time to devote to breeding and are more productive as a consequence. Consistent both with von Haartman's and with Greenberg's views is a recent report by Schwabl (1983) that sedentary male European blackbirds ***Turdus merula*** are more productive than migrants, evidently because they become territorial before migrants return to breed and therefore are able to occupy better breeding territories and also to begin breeding earlier, when nest success is high. Migratory blackbirds, Schwabl suggests (citing Lack), may compensate for their loss of productivity by higher annual survivorship.

For the junco's differential migration, we proposed (1983a) a hypothesis that, like Lack's (1954, 1968), both emphasized differences in winter mortality according to location of the winter residence and also treated migration as an important cause of mortality. But whereas Lack emphasized that survivorship of migrants and non-migrants balances out only over the years, we proposed for juncos that equalization between the survivorship of long- and short-distance migrants might occur over the winter and migration seasons, i.e., within a single year. This argument is developed below.

Table 1
The effects of migration distance and wintering latitude on passerine population dynamics (after Greenberg 1980).[a]

	Adult Annual Survivorship $\bar{x}$ of (*n* spp)	Annual Productivity[b] $\bar{x}$ of (*n* spp)
Long-distance migrants overwintering in subtropics or tropics	57% (14)	2.68 (13)
Residents, partial migrants overwintering in temperate zone	47% (14)	5.14 (5)

a = Data summarized from Tables 1 and 2, Greenberg (1980). Where Greenberg listed several estimates for the same species, we averaged these to produce a single estimate.

b = Number of young leaving nest, on season-long basis, per female adult.

Finally, Baker (1978), drawing on ideas of Fretwell (1972), reasoned that variation in the migrations of population classes may continue indefinitely despite inequality of fitness among the classes. If winter occupancy of a certain region leads to greater productivity without associated decrease in probability of survival, and if the winter resources of the region are insufficient to support the entire population, one or more classes may be more successful than the other(s) in controlling these resources. In this despotic situation (Fretwell 1972), the less successful birds will migrate if to do so raises their expected fitness above the level that is probable if they do not migrate. This model may account for cases in which adults are dominant over young and are sedentary or make short migrations while young make longer movements (see Gauthreaux 1982 and this volume). Thus Hilden (1982) found that in the partially migratory Finnish goldcrest (***Regulus regulus***), adults, which are dominant over young, tended not to migrate and young to migrate. Winter mortality of migrants and non-migrants was equal, but non-migrants were more productive because they were able to occupy the best territories, doing so before migrants returned in spring. Because migratory behavior differences were associated with age (an individual's behavior changed as it grew older), Hilden regarded genetic polymorphism as an unlikely mechanism to account for his data. The age difference in migratory behavior could be proximately caused (Pulliam and Parker 1979; Gauthreaux 1978, 1982); e.g., young might migrate only as the result of direct interactions with adults (Hilden 1982). Or, if it were almost invariably advantageous for young to migrate, selection may have produced a developmental program having that obligate result.

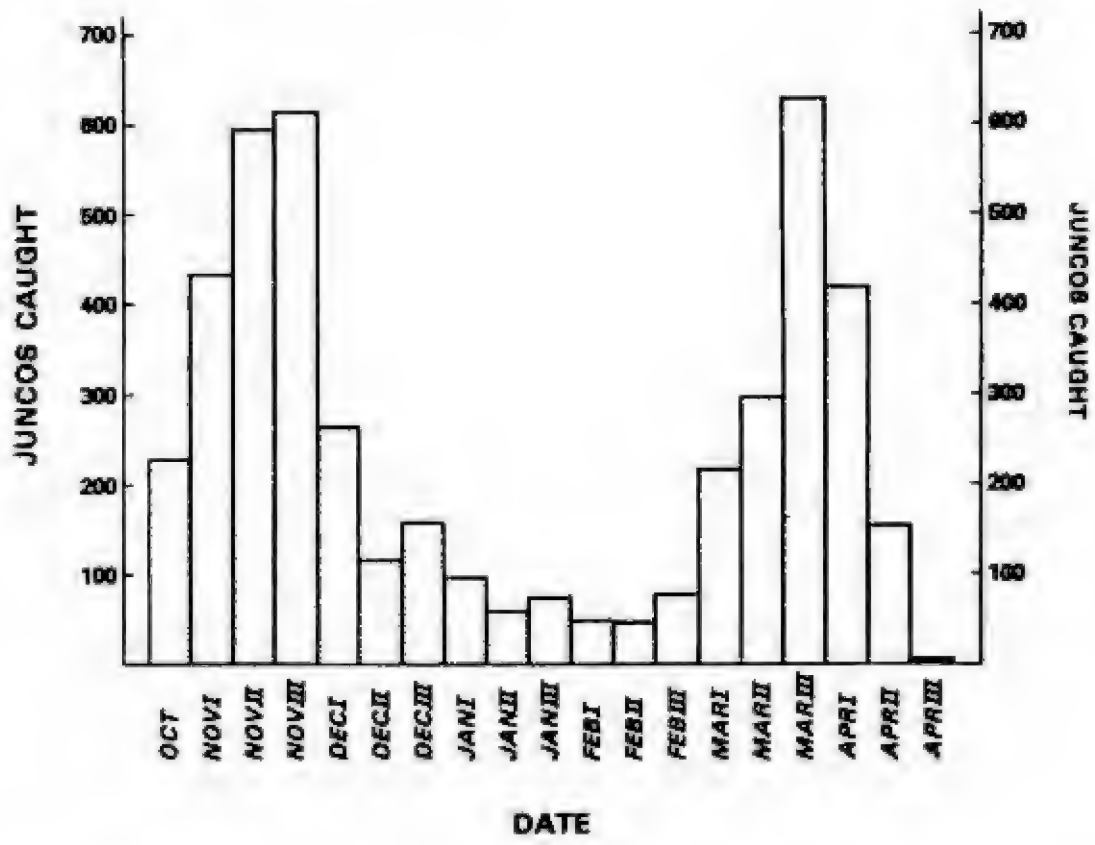


Figure 1

Dates of first capture in southern Indiana of 4550 individual juncos, according to approximately ten-day intervals, four years pooled. Capture efforts were approximately equal at all dates in all years.

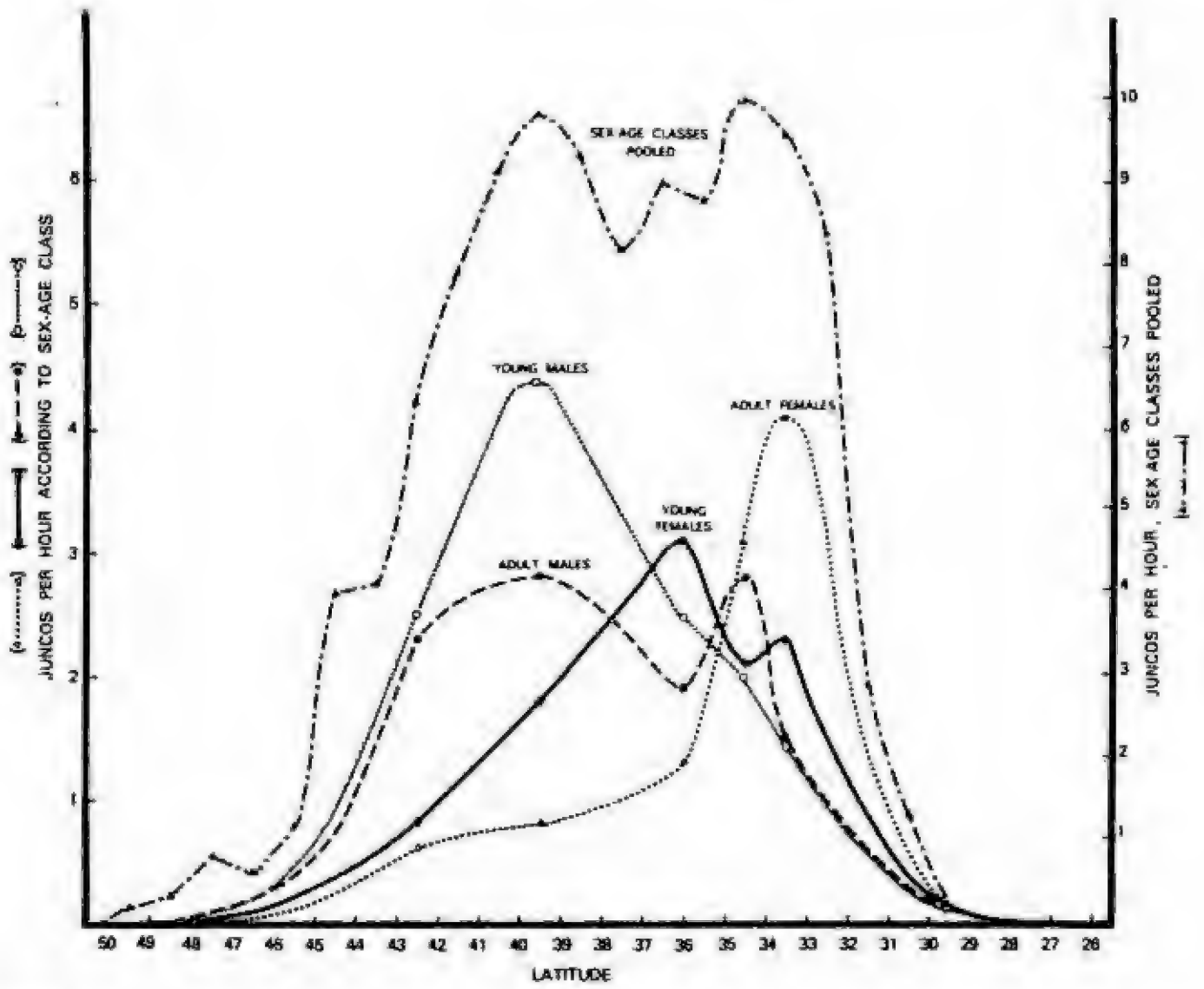
Sexual differences in migratory behavior would seem to provide the special case. Because fitness of the sexes is equal by definition, any sexual differences in average survivorship (e.g., Prŷs-Jones 1977) would have to be made up in average productivity. Males, if despotic over females, might be more likely than females to survive winter, but their chances of obtaining a mate might then be decreased, and differences in migratory behavior could persist.

Because of the rarity of demographic data relevant to these hypotheses, we summarize data for the dark-eyed junco, despite their gaps, and describe our view of the evolution and maintenance of differential migration in that species.

DIFFERENTIAL MIGRATION IN THE DARK-EYED JUNCO

The dark-eyed junco breeds principally in Canada and winters in the United States. In the eastern United States where our field work has focused, autumn migration is first detected in September, reaches its peak at the middle latitudes of the winter range in November, and concludes by about 1 December (Fig 1). Spring migration takes place between about 1 March and early May (Fig 1).

In winter, female juncos are found, on average, farther from the breeding ground than males, and within each sex, adults (birds in the second or later winter of life) tend to be located south of young produced in the preceding breeding season (Fig 2). Males dominate females at food sources in winter, and adults dominate young of their sex (Balph 1978, Baker and Fox 1978, Ketterson 1979). Body size varies in the


JUNCOS PER HOUR ACCORDING TO SEX-AGE CLASS
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YOUNG MALES
ADULT FEMALES
YOUNG FEMALES
ADULT MALES
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26
LATITUDE

Figure 2

Estimated relative abundance of juncos in the winter range (top curve) and estimated relative abundance of the sex and age classes (lower series of curves), all according to degree of latitude (from Ketterson and Nolan 1983a; reprinted by permission from Current Ornithology, Volume 1, Copyright 1983, Plenum Publishing Company).

same order, and the differences in body size appear to cause the correlation between dominance rank and sex and age (Ketterson 1979). Juncos are monogamous, and our field observations (unpublished) indicate that individuals of both sexes regularly breed as yearlings.

The breeding origins of winter populations are unknown, but we conclude from the winter distribution that (1) females make longer migrations, on average, than males, and (2) adults make longer migrations than young. Conclusion (1) assumes either that the adult sex ratio in the breeding range is invariant with latitude or, if it is not, that the proportion of breeding adult females does not decrease toward the north. Conclusion (2) assumes either that the ratio of young to adults just preceding fall migration is invariant with latitude or, if southern breeding populations produce more young per adult, that the migration of juncos is not of the leap-frog type. Evidence to date is against the possibility that breeding populations tend to remain intact in the winter range, which would be the effect produced by leap-frog migration. Reasons for thinking instead that breeding populations intermingle in winter are detailed elsewhere (Ketterson and Nolan 1982). Figure 1 thus reveals, we believe, that the junco is a

differential migrant according to both sex and age and also that individuals within a class differ considerably in distance migrated.

The winter distribution is repeated year after year, and we have considered (Ketterson and Nolan 1982, 1983a) whether either Lack's or von Haartman's arguments, extended to differential migration, could account for this annual stability. That is, does the annual mortality rate of long- and short-distance migrants fluctuate around a mean that is the same for both migratory categories (Lack)? Or is mortality consistently higher in either short- or long-distance migrants, suggesting that productivity varies in a compensatory way to produce equal fitness (von Haartman)? Or, as described by Fretwell (1972) and Baker (1978), is mortality density-dependent and the situation, despotic, such that the fitness of the migratory categories need not be equal? Because our long- and short-distance migrant populations (i.e., southern and northern winterers) differ in sex and age composition, the first step in seeking the answer to these questions is to ask whether sex and age affect survivorship among southern and northern winterers. Therefore we begin our analysis by making within-population sex and age comparisons.

Comparison of Sex-Age Classes Wintering at the Same Location

If young juncos that winter at higher latitudes were to survive the period from December to December at the adult rate (ca. 50%, Table 2) and if in the second December of life all survivors from the preceding year returned to their first-year wintering latitudes, the observed annual surplus of young juncos in the north could not be maintained. Instead, the proportion of adults to young would be 50:50 throughout the range. Since the proportions do vary year after year from north to south, either (1) annual survivorship is lower among northern-wintering first-year juncos than among northern-wintering adults, or (2) survivors among northern-wintering first-year juncos tend to travel farther southward in their second autumn migration when they are adults, or (3) both. The annual rate of return to (recapture in) the north by juncos banded there as young is lower than the rate of return there by those banded as adults (Table 3, point A1). This could be seen as support for either possibility (1) or (2), but for several reasons we believe that northern-wintering young probably survive the period December-to-December as well as do northern-wintering adults. First, in each of two winters at northern, midrange, and southern latitudes, the sex-age ratios of samples of junco populations (n ca. 1300) caught in early winter remained constant until winter's end (Table 3, point A2). This absence of overwinter change suggests strongly that first-year birds, regardless of sex, survive winter (a season when young birds might still be at special risk because of inexperience and probably the limiting season for juncos) as well as do adults at the same place. Second, in two winters and at two locations (northern and southern), the likelihood that a bird captured and banded in early winter (n = 335) would be recaptured at the same site in late winter was independent of sex and age (Table 3, point A3). This too points to equal overwinter survivorship among the sex-age classes. As for possibility (2) above—that some individuals migrate farther southward when adult than when young—U.S. Fish

and Wildlife Service data on juncos banded throughout the eastern United States in one winter and recovered at a different location in a later winter, reveal a tendency for the recovery location in the later winter to lie south of the location in the first, sometimes much farther south (Table 3, point B4). Although the sex and age of these birds were unknown, this observation is also consistent with the possibility that some young birds that spend the winter in the north form no bond to the first winter site, i.e., do not develop fidelity that would cause the survivors among them to return in the following year.

Comparisons of Populations at Northern and Southern Locations

The apparent absence of sex-age associated differences in survival of juncos at the same location (above) permits us to pool data from each location without respect to sex or age, then to compare populations across locations. That is, we are in a position to ask what the demographic consequences of long- as opposed to short-distance migration may be.

Within-Winter Mortality—The recapture rate in late winter of juncos banded early in that same winter is considerably greater in the south (n = 136) than in the north (n = 198; Table 3, point B1). This suggests that overwinter survival of southern juncos is higher than that of northern, but it is also consistent with the possibilities that dispersal from the banding site is lower in the south or that both survival and dispersal vary with latitude. U.S. Fish and Wildlife Service records indicate no lower within-winter dispersal in the south (Table 3, point B2), although these records are summarized in a way that would not reveal geographic differences in movement over very short distances. We suspect that northern-wintering juncos are, in fact, likely to have larger home ranges than those in the south, because food is more patchily distributed when snow and ice cover the ground, as is more frequently the case in the north. But this climatic difference also makes it highly probable, and there is anecdotal evidence, that winter mortality is greater in the north.

Annual Mortality—Despite the geographic difference in within-winter recapture rates, annual rates of return (year-to-year recapture rates) of adults to the north (n = 279) and the south (n = 171) are statistically invariant (Table 3, point B3). This leads us to propose that annual mortality is independent of latitude of the wintering site. A corollary hypothesis is then that mortality rates at some season(s) other than winter also vary with wintering latitude, i.e., that compensating seasonal rates account for the geographical equality among annual rates. If southern-wintering juncos suffer high non-winter losses that balance out their greater survivorship during winter, it is most probable that these losses occur during and as a result of their longer migrations. It follows that all sex-age classes, regardless of wintering location, could survive equally well in the 12 months between one December and the next. Further, it is unnecessary to hypothesize, as the basis for the winter distribution, either variation in productivity correlating with distance migrated or the existence of a despotic situation. In offering

Table 2

Independent estimates place annual survival of adult juncos at approximately 50%

1.	Based on return rate of of male juncos to former breeding territories, Wawa, Ontario[a]	53% $n = 49$
2.	Based on return rate of juncos already known to be site-faithful to wintering area, males and females, in Bloomington, Indiana.[b]	53% $n = 128$
3.	Based on interval between banding and recovery among birds banded in one winter and recovered in a later winter, USFWS data.[c]	54% $n = 85$
4.	Based on proportion of adult birds present at beginning of winter.[d]	$\geq$ 46%

a = Ketterson and Nolan 1983a, plus additional data. Included were birds known to be territorial in one year and to have returned in the following year. Data were gathered in summers of 1981, 1982, and 1983.

b = Ketterson and Nolan 1982, p. 250.

c = Ketterson and Nolan 1982, Table 5.

d = Ketterson and Nolan 1983a, planimetry of Figure 2. We summed the areas under the sex-age curves and computed the percentage of that sum contributed by adults. In a stable population, the age structure would correspond to survivorship.

this view, we emphasize two points. First, we expect that the mortality of young between attaining independence and beginning fall migration exceeds that of adults (Perrins 1980) and that their death rate continues to be higher during migration (Greenberg 1980). But those still alive in December, at the conclusion of migration, appear to have passed beyond the period of special risks stemming from youth (compare the similar findings for the great tit *Parus major*, Perrins 1980). Second, we do not argue that populations from different wintering latitudes invariably experience equal annual mortality, i.e., that seasonal mortality rates of winter populations balance out every 12 months. We wish only to point out that equalization

Table 3

Summary of junco population dynamics[a]

A. Within population comparisons at wintering sites:

1. Annual return rates differ geographically and, at a single location, according to age. In the north, adults are more likely than young to return the following year. In the south, return rates are equal.
2. Sex-age ratios differ geographically, but at a single location they do not change from early to late winter.
3. Frequency of recapture at end of winter of individuals marked in early winter differs geographically, but at a single location it is independent of sex and age.

B. North-south comparisons across wintering populations:

1. Late-winter recapture of birds banded early in same winter are significantly greater in south than in north.
2. USFWS recovery data do not indicate geographic variation in mid-winter dispersal.
3. Annual return rates to north and south are equal among adults.
4. USFWS recovery data indicate that northern-wintering juncos are more likely to move between seasons; moves tend to be southward.
5. Annual return rates among young are lower to north than to south.

C. Interpretation:

1. Beginning in early winter, survival at a wintering site is sex- and age-independent.
2. Southern-wintering juncos survive winter at a higher rate than northern-wintering juncos.
3. Southern-wintering juncos apparently experience higher migration mortality than northern-wintering juncos.
4. Annual survival from one early winter to the next does not differ north to south.

[a] After Ketterson and Nolan 1982, 1983a.

of mortality rates appears, among juncos, to be capable of taking place over shorter time intervals than the long periods proposed by Lack (1954, 1968).

Interspecific Comparisons—Is there inconsistency between this hypothesis and that of Greenberg (1980), who also emphasizes variation in overwinter survivorship but finds compensation in countervailing variation in productivity rather than mortality associated with distance migrated? Given that Greenberg was concerned with

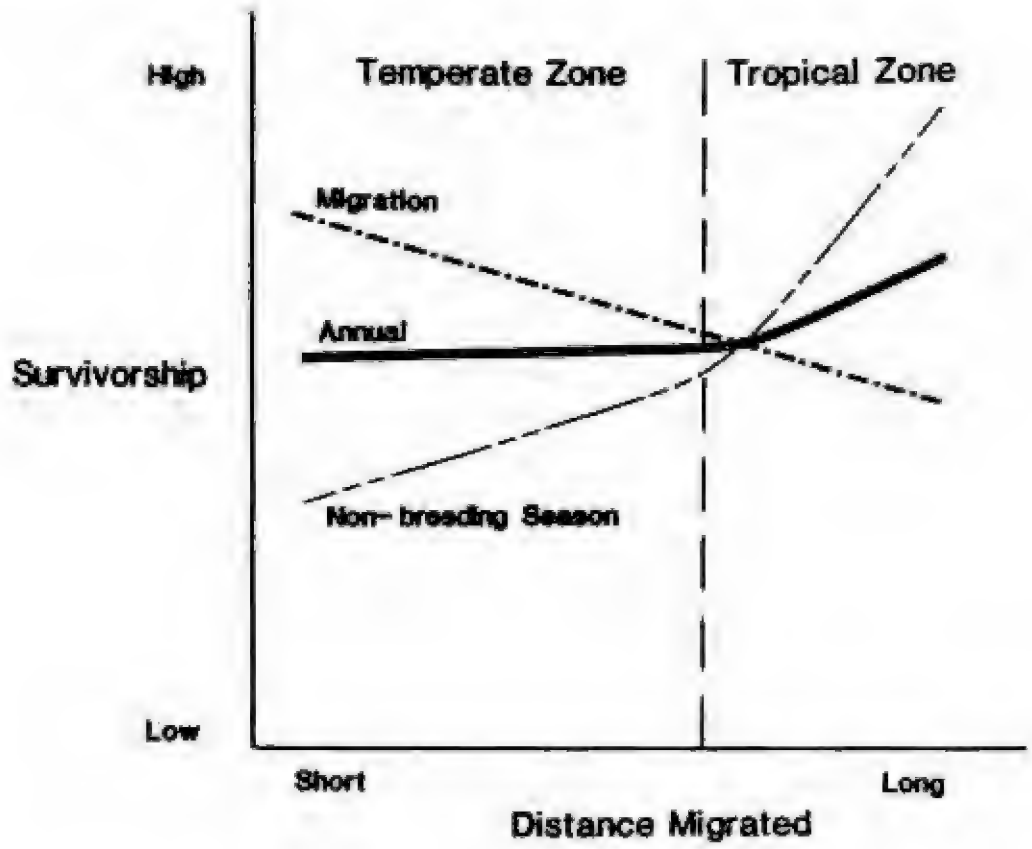


Figure 3

Schematic hypothetical representation of the manner in which temperate- and tropical-wintering passerine bird species that breed in the temperate zone might differ with respect to the interaction of winter and migration mortality resulting in variation in annual survival among species.

interspecific differences and therefore could not control for many variables that are automatically controlled for in within-species comparisons, there is no necessary tension between the two models. Nevertheless, because of the importance we attach to the relationship between migration distance and migration mortality, we ask how tropical-wintering passerines that make longer migrations than juncos can exhibit higher annual survivorship. If the slope relating migration distance to migration mortality is shallow, whereas the function relating migration distance to winter survival is steep or sharply curvilinear (as depicted hypothetically in Figure 3), tropical migrants could experience higher annual survivorship than temperate-zone migrants, even though the two groups suffered comparable mortality per unit distance traveled during migration.

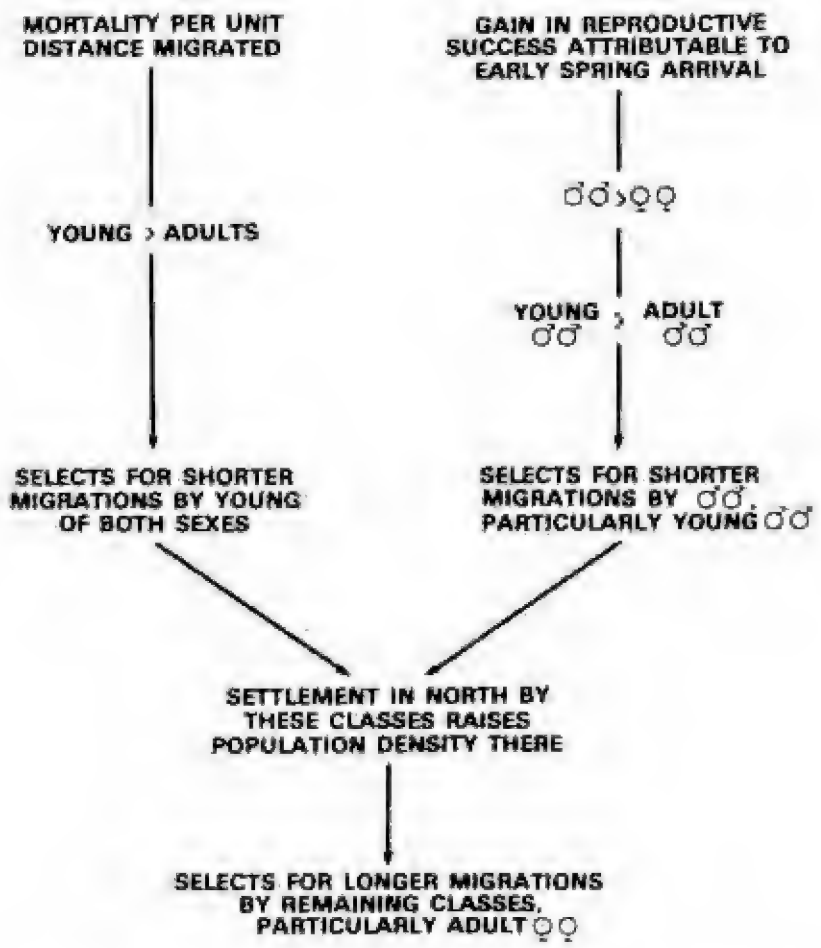
WHY SEX-AGE DIFFERENCES IN TENDENCY TO MIGRATE OR IN DISTANCE MIGRATED?

If male and female juncos, young and adult, survive equally well from winter to winter regardless of distance separating breeding and wintering sites, what ultimate factors might be responsible for the observed sex-age differences in migratory distances? If we assume that average survivorship or productivity of the members of the various classes would decrease were they to behave other than they do (Ketterson and Nolan 1983a), then the question is not only what the ultimate factors are, but how they may differ in their impact according to class. Recent reviews addressing these

questions (Gauthreaux 1978, 1982 and this volume; Baker 1978; Greenwood 1980; Myers 1981; Ketterson and Nolan 1983a) have proposed as ultimate factors a number of social and other environmental variables, among them: (1) breeding-season social organization, including whether males defend territories (i.e., resources) or mates (Greenwood 1980), and degree of intrasexual competition for breeding resources (Myers 1981); (2) non-breeding-season social organization, including the extent to which family units remain together, thus precluding partial or differential migration (Emlen 1978), and the impact of any interclass differences in competitive status arising out of dominance (Gauthreaux 1978, 1982, this volume); (3) sex- or age-related differences in physiological tolerance of severe weather or in costs of migrating (Ketterson and Nolan 1983a); or (4) some combination of the above (Baker 1978, Ketterson and Nolan 1983a). For example, in an effort to account for a sexual difference in a species' migratory behavior, it might be supposed that something about the breeding social organization (e.g., a monogamous mating system, with males territorial) would cause the productivity of the average male to decline if he were to winter farther from the breeding ground. To females, non-breeding social organization might be of paramount importance. If females suffered dominance-related disadvantages when overwintering with males, selection might favor longer migrations by females.

Applying these notions to the junco, we have identified (Ketterson and Nolan 1983a) as the selective factors most likely to have affected the sex-age classes differentially: (1) the likelihood of death during migration, (2) the importance of early return to the breeding ground, and (3) the advantage of avoiding high densities of conspecifics (Fig 4). Factors (1) and (2) would favor shorter migrations, and factor (3), because the winter range apparently fills from north to south, would favor continuation of migration southward (Pulliam and Parker 1979). Shorter migrations by young are probably primarily attributable to factor (1) because the probability of death per unit distance migrated is doubtless higher during their first autumn than ever again in their lives (Ralph 1971, Nolan 1978, Greenberg 1980). On the other hand, factor (3) may have been predominant in the evolution of the adult pattern. That is, individuals of any class moving southward would be likely to experience the advantages stemming from escaping high population densities (Pulliam and Parker 1979); but if the costs of extending the migration were lower for adults, it is they that would be expected to keep moving. Factor (1) probably accounts for the sexual differences observed. Young males, never having occupied a territory and soon to require one if they are to breed, are likely to benefit most from early return. But males, regardless of age, must have territories before females arrive, or they will at best have abbreviated opportunities to reproduce.

What of the role of dominance? In the present state of knowledge, dominance alone cannot account for the junco's migration pattern. Adults are dominant to young, yet they tend to make longer migrations, and at none of the sites we studied did the dominant sex or age class appear more likely than the subordinate ones to survive winter. It is possible, however, that those adults that settle south of young did in fact


MORTALITY PER UNIT DISTANCE MIGRATED
GAIN IN REPRODUCTIVE SUCCESS ATTRIBUTABLE TO EARLY SPRING ARRIVAL
♂♂>♀♀
YOUNG > ADULTS
YOUNG ♂♂ > ADULT ♂♂
SELECTS FOR SHORTER MIGRATIONS BY YOUNG OF BOTH SEXES
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SETTLEMENT IN NORTH BY THESE CLASSES RAISES POPULATION DENSITY THERE
SELECTS FOR LONGER MIGRATIONS BY REMAINING CLASSES, PARTICULARLY ADULT ♀♀

Figure 4

Selective factors proposed to account for the differential winter distribution of the dark-eyed junco in eastern North America (from Ketterson and Nolan 1983a; reprinted by permission from Current Ornithology, Volume 1, Copyright 1983, Plenum Publishing Company).

extend their migrations because they were unable to dominate those young. That is, investigations of sex- and age-related dominance rarely consider the histories of individuals making up the population sampled, and the young members of the sample may already have excluded some potential adult settlers before the investigation began. Alternatively, the distribution of adult males might be explained as the hyperdispersion of those individuals that are a priori most likely to be at the top of a dominance hierarchy. However, in our opinion, until more is known of the relationships between rank in a hierarchy, ability to defend resources, and tendency to disperse or migrate, further speculation would be premature.

REGULATION OF DISTANCE MIGRATED

Introduction

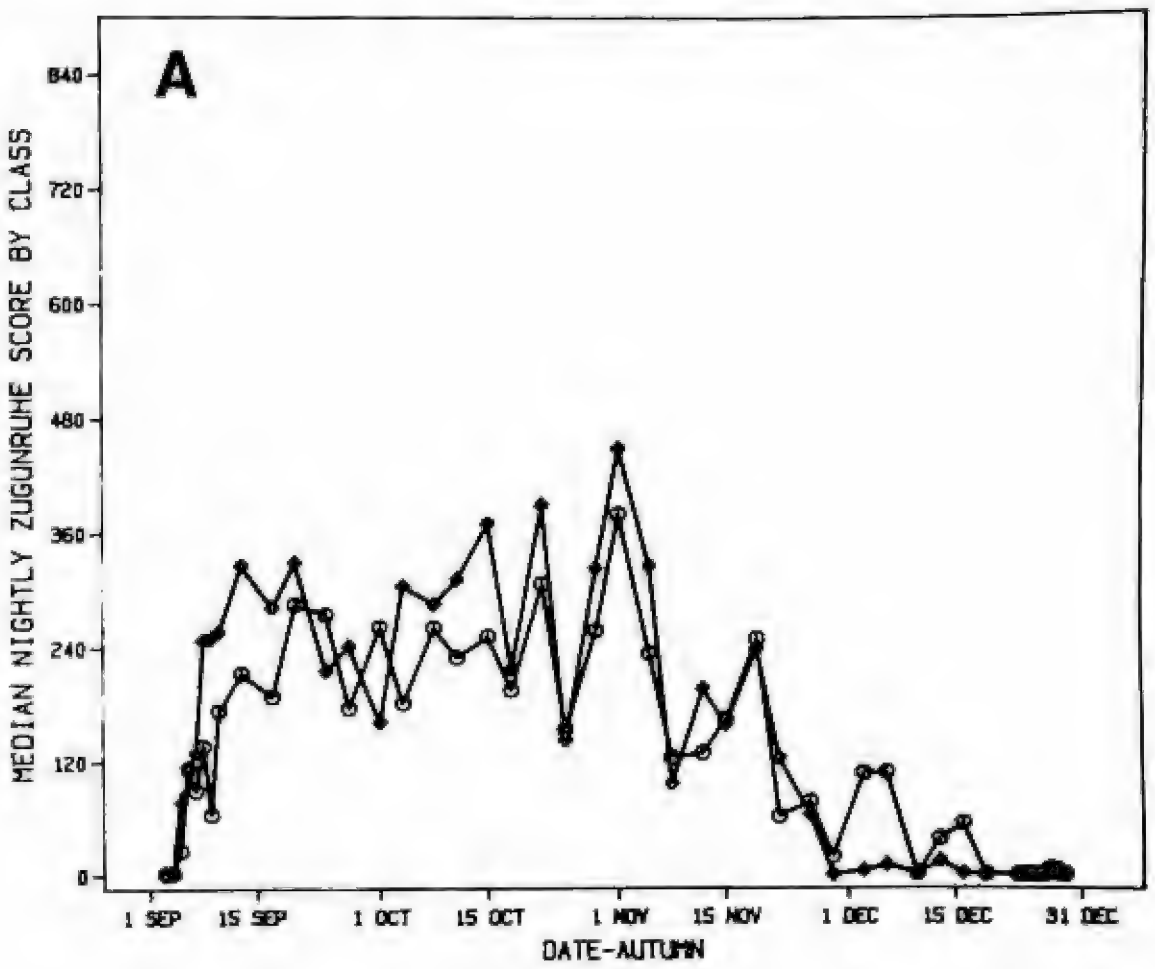
The importance of an endogenous program in regulating the distance traveled by first-time migrant European warblers *(Phylloscopus spp.)* was first suggested (Gwinner 1968) by the discovery of a correlation between (1) levels and proportions of zugunruhe (migratory restlessness) in caged, inexperienced birds and (2) distance covered toward the winter range during the same time interval by migrating conspecifics. Since that discovery, comparative studies and more recently breeding

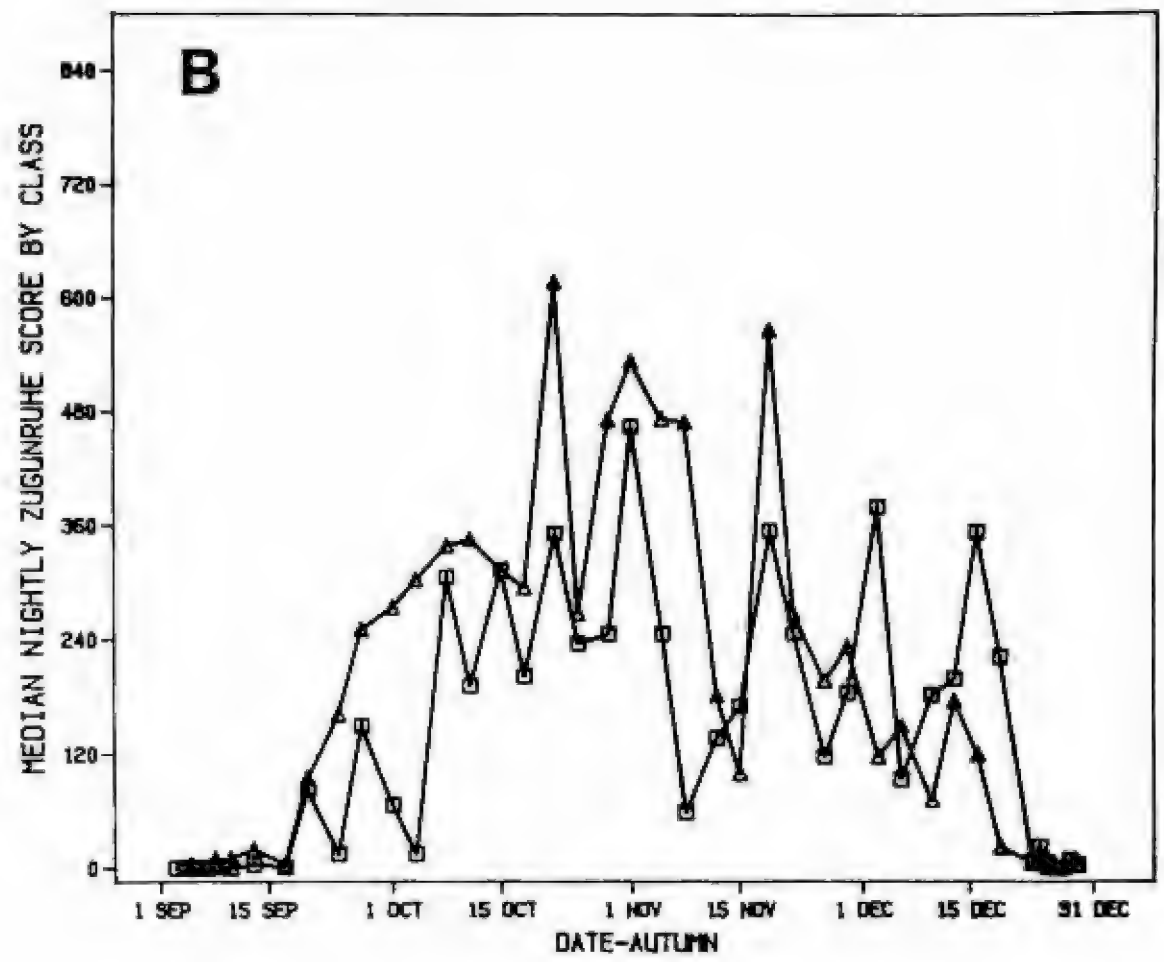
experiments have made a persuasive case for the endogenous nature of inter- and intraspecific variation in the duration, intensity and orientation of zugunruhe in a number of sylviids and in several other species as well (Berthold 1973, 1977 and this volume; Gwinner and Wiltschko 1978, 1980; Berthold and Querner 1981, 1982; Biebach 1983; Schwabl 1983). The endocrine basis of these differences is still not well understood, though a report by Schwabl, Wingfield and Farner (1984) represents recent progress.

Thus, in some species, distance migrated may be determined largely by a genetically defined time period during which the individual is in the migratory physiological state. During this period, the bird moves in the seasonally appropriate direction at the rate of speed typical for the species, and when the period expires, it quits migrating—at a latitude to which it is adapted, assuming that its program has functioned properly.

In other species, migratory behavior evidently is more strongly modified by experience during previous migrations or by conditions met in the migration then in progress. For example, experience in migrating into the normal winter range was found to play a major part in determining both direction of flight and distance traveled by European starlings *(Sturnus vulgaris)* captured during fall migration and displaced from their normal pathway. Young of the year did not correct for the displacement, whereas many adults did correct and headed back to the winter destination appropriate for the population, where presumably they had spent the previous winter(s) (Perdeck 1958, 1967). Food abundance along the route of migrating sparrows has been shown to affect winter distribution; some migrants travel farther into the winter range under certain food conditions than under others (Pulliam and Parker 1979), with a consequent effect on winter population densities. If food supplies of yellow-rumped warblers *(Dendroica coronata)* fail in midwinter, migration may resume (Terrill and Ohmart 1984). Gauthreaux (1978, 1982, this volume) has argued that dominance relations among transients play a proximate role in determining distance migrated. That is, individuals that are the frequent butt of aggression may experience food deprivation, become hyperactive (Merkel 1966, Ketterson and King 1977, Stuebe and Ketterson 1982, Terrill, personal communication), and migrate farther toward a more favorable social environment. Even among species that migrate a distance fixed within fairly narrow limits set by endogenous mechanisms, it seems likely that toward the end of the individual's migration the site selected as the stopping point is influenced to some degree by external environmental conditions (see also Terrill and Ohmart 1984).

Curious about the extent to which the junco's winter distribution is the result of endogenous as opposed to exogenous factors, we measured zugunruhe in young and adults of both sexes taken from a single breeding population. Our rationale was that if sex-age differences in the duration and intensity of nocturnal restlessness correlated with differences in distance migrated, i.e., if adults were more active than young of their sex and females more active than males of their age in both autumn and spring, then some role for an endogenous program would be indicated. Such an observation would open the possibility of a sex-linked genetic basis for the differential migration


A
MEDIAN NIGHTLY ZUGUNRUHE SCORE BY CLASS
840
720
600
480
360
240
120
0
1 SEP
15 SEP
1 OCT
15 OCT
1 NOV
15 NOV
1 DEC
15 DEC
31 DEC
DATE-AUTUMN


B
MEDIAN NIGHTLY ZUGUNRUHE SCORE BY CLASS
840
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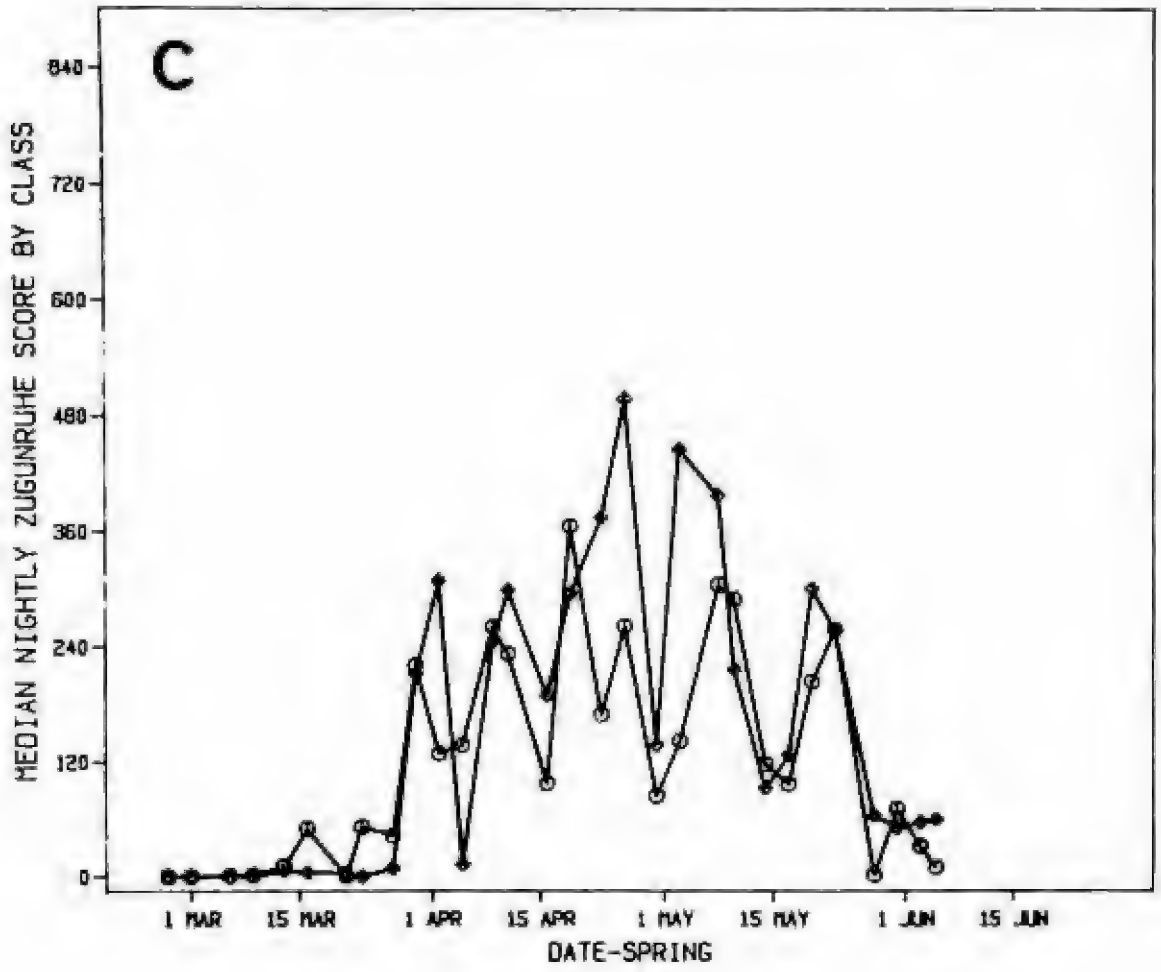

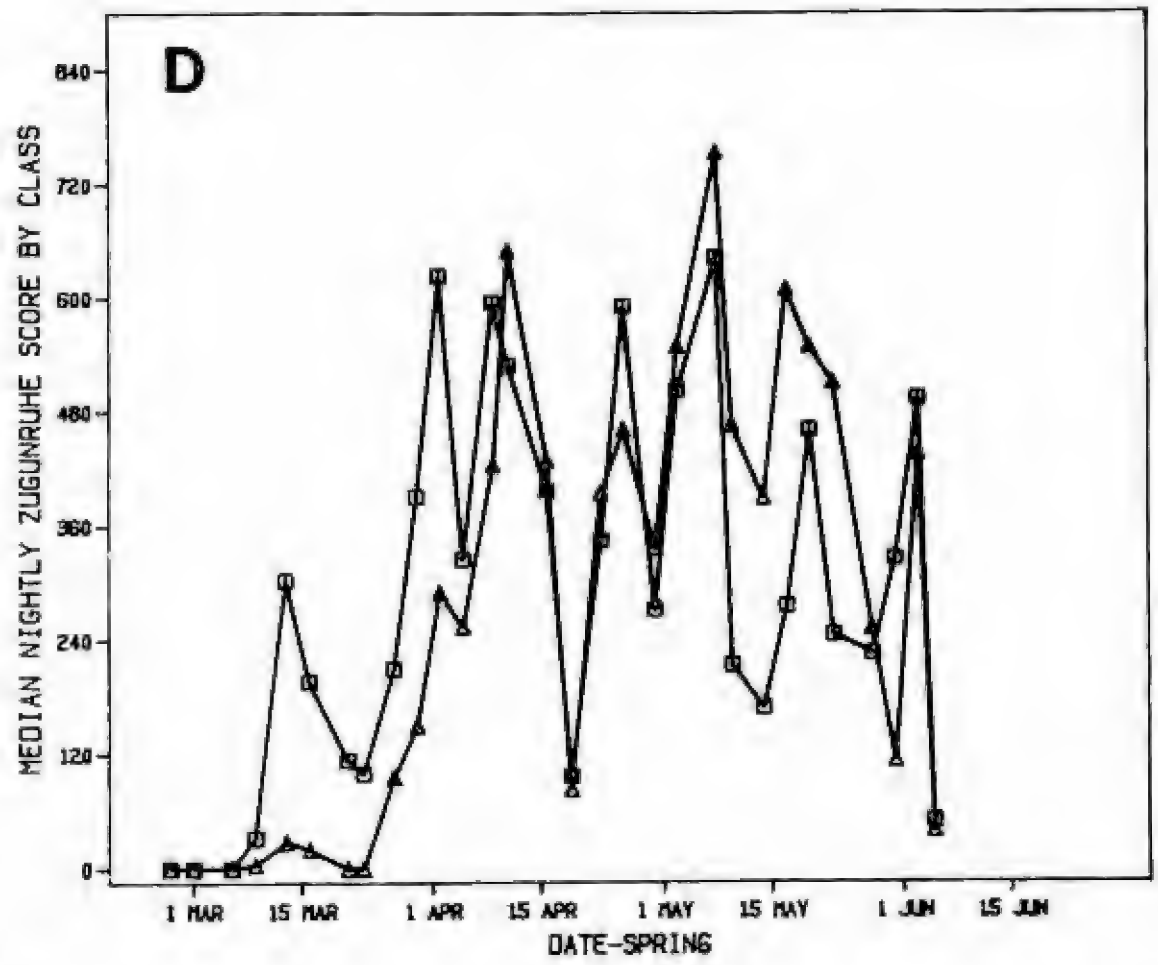

Figure 5

Median nightly zugunruhe score (number of 30-second intervals with activity between 2100 and 0430) according to date (activity determined two nights per week), season, and sex-age class. (Young males, $n = 19$ in autumn, 9 in spring, circles; young females, $n = 14$ in autumn, 7 in spring, diamonds; adult males, $n = 8$ in autumn, 3 in spring, squares; adult females, $n = 9$ in autumn, 6 in spring, triangles.) (A) upper, facing page: young in autumn; (B) lower, facing page: adults in autumn; (C) upper, above: young in spring; (D) lower, above: adults in spring.

of this species and/or of a genetically based developmental program. If the classes did not differ, we might conclude that external factors were the important ones in determining the winter distribution. To our knowledge, this is the first effort to address this question in a differential migrant.

Methods

Because our methods have already been described (Ketterson and Nolan 1983b), we refer to them only briefly. Breeding adult juncos and still-dependent or newly independent young in juvenile plumage (hereafter, adults and young) were captured at Wawa, Ontario, Canada (48°00′N, 84°50′W), between 21 July and 28 July 1980, transported to Indiana (39°50′N, 87°30′W), and throughout autumn 1980 were individually caged outdoors in visual isolation from each other. Subjects then spent January–February 1981 together in large outdoor aviary cages, after which they were returned to individual cages. Each such cage was equipped with a single perch attached to a microswitch connected to an Esterline-Angus event recorder. During two nights each week in the periods September–December and March–June, we counted the number of 30-second intervals during which an individual was active (i.e., left or landed on its perch at least once) between 2100 and 0430 hours. These values constituted nightly zugunruhe scores, and the sums of nightly scores in autumn and spring yielded seasonal scores. In each season we counted the number of nights on which an individual's nightly score was equal to or greater than 60, treating such nights as active nights. An individual's average activity per night was determined, again in each season, by dividing the total of its nightly scores on all active nights by the number of its active nights. To relate zugunruhe to calendar date in autumn, we noted for each bird the dates of its first and last active nights and the date by which it had accumulated half its total seasonal score. Because captive juncos, like many other species (Gwinner and Czeschlik 1978), prolong nocturnal restlessness beyond the normal dates of migration in spring, in that season we established only each individual's starting date (its first active night).

Results

The median nightly zugunruhe scores of each sex-age class according to date (Fig 5) indicate that in general the timing of zugunruhe corresponded to the timing of migration of free-living birds (Fig 1). Day-to-day variation in nightly totals correlated with varying weather conditions that are generally accepted as facilitating or suppressing migration, e.g., zugunruhe was reduced or absent on rainy and stormy nights. Inspection of Figure 5A and B, reveals several trends in autumn:

1. young juncos (5A) appear to have begun and ended zugunruhe at earlier dates than adults (5B),
2. nightly totals appear to have been greater in adults than in young, and
3. sexual differences were slight, with females tending to be more active than males early in the season and males more active than females later in the season.

Table 4

Three measures of zugunruhe; median values according to sex, age and season.

	Autumn[a]		Spring[a]	
	Males	Female	Males	Females
Number of Active Nights[b]				
Young	23.7	21.0	15.8	18.3
Adults	21.0	23.0	23.0	20.5
Activity per Night[c]				
Young	247	292	229	272
Adults	272	361	453	432
Seasonal Total[d]				
Young	5,594	5,754	4,072	4,522
Adults	6,314	9,417	10,861	8,842

[a]Sample sizes in autumn were 19 young males, 14 young females, 9 adult males, 8 adult females; in spring there were 9 young males, 7 young females, 3 adult males, 6 adult females.

[b]In autumn, 35 nights were scored; in spring, 29. Given is median number according to class, of nights when nightly score ≥ 60.

[c]Maximum possible nightly score is 900. Given is median score, according to class, of average activity on active nights.

[d]Maximum possible in autumn was 31,500 (35 nights $\times$ 900 possible per night), maximum possible in spring was 26,100 (29 $\times$ 900). Given is median value, according to class, of seasonal total.

In spring (Fig 5C and D), adults (5D), particularly males, became restless earlier than young (5C), and nightly totals were again greater in adults than young.

Table 4 presents, for both seasons and according to class, the median values of number of active nights, of average activity per night, and of total seasonal scores. In this paragraph we refer only to the autumn data. Recognizing that the seasonal score is not independent of the number of active nights and activity per night, we compared for each of these three variables the median values of young males vs. young females, adult males vs. adult females, young males vs. adult males, and young females vs. adult females. In these twelve comparisons, results of ten were in the direction predicted by the winter sex-age distribution. Despite this, few statistical tests permit rejection of the null hypothesis that the classes did not differ (Table 5). For number of active nights, classes were statistically indistinguishable. For average activity per night, adult females were more active than adult males, but other comparisons showed no differences. For seasonal scores, adult females accumulated higher totals than young females. One pattern was clear (Table 6): age determined the calendar

Table 5
Results of statistical comparisons according to sex and age[a,b].

		Number of Nights	Activity/Night	Seasonal Total
Autumn 1980				
Age	Young male/adult male	n.s.	n.s.	n.s.
	Young female/adult female	n.s.	$p < 0.10$	*
Sex	Young male/Young female	n.s.	$p < 0.10$	n.s.
	Adult male/Adult female	n.s.	*	$p < 0.10$
Spring 1981				
Age	Young male/Adult male	*	*	*
	Young female/adult female	$p < 0.10$	n.s.	*
Sex	Young male/young female	n.s.	n.s.	n.s.
	Adult male/Adult female	n.s.	n.s.	n.s.

[a]Mann-Whitney U; * signifies one-tailed $p < 0.05$; n.s. signifies one-tailed $p > 0.10$.

[b]See text for definitions of variables.

schedule of restlessness, with young birds, regardless of sex, beginning and ending their autumn restlessness some two weeks ahead of adults.

Turning to spring, nine of twelve comparisons were in the predicted direction (Table 4), and despite the small samples, several comparisons were statistically significant (Table 5). Adults became active significantly earlier (Table 6) and therefore tended to accumulate more active nights than young, and among males, adults were more active per night. In both sexes, adults had higher seasonal scores. None of the sexual comparisons produced statistically significant differences.

Interpretation

If zugunruhe reflects a state of readiness to migrate, in autumn that state lasts approximately 85 days among juncos from the Wawa, Ontario, breeding population, regardless of sex-age class (Table 6). During this period these birds would probably migrate only on nights when weather conditions are favorable (Muller 1976, Richardson 1978) and energy stores adequate. Temporal variation in the occurrence of zugunruhe suggests that first-time migrants may begin and end migrating earlier i.e., may arrive at the winter site before adults. Thus adults, which undergo a complete molt after reproducing, may delay departure from the breeding range longer than

Table 6
Onset and termination of zugunruhe according to sex-age class.[a]

	Autumn			Spring
	First Date ≥ 60	50% Date	Last Date ≥ 60	First Date ≥ 60
Young males	7 Sept	18 Oct	9 Dec	29 Mar
Adult males	20 Sept	5 Nov	16 Dec	12 Mar
Young females	7 Sept	18 Oct	30 Nov	26 Mar
Adult females	19 Sept	1 Nov	16 Dec	26 Mar

[a]Median date, according to class, of individuals' first and last nights when nightly score ≥ 60 and date by which 50% of the seasonal total score had been accumulated. Age classes differed significantly (sexes combined, Mann-Whitney U, one-tailed $p < 0.001$ for starting date in autumn; $p < 0.05$ for ending date and 50% date in autumn and for starting date in spring). Sample sizes as in Table 4.

young (particularly early-brood young), which do not molt the remiges or the rectrices in acquiring the first basic plumage. If adults do migrate later, young might have the opportunity to establish some measure of site-related dominance on their winter home range based on their earlier arrival, i.e., prior residence (Balph 1979, Yasukawa and Bick 1980). Later-arriving adults may possess mechanisms that enable them to assess population densities and resources which are likely to be available in the coming winter at stop-over points and to react, either by migrating farther or by settling (Pulliam and Parker 1979). Alternatively, the earlier zugunruhe of young may correspond to late-summer and early-autumn movements having no southward orientation among free-living young of the year (Baker 1978, p. 630); in that case it would not translate into earlier arrival in the winter range.

Preliminary analysis of first-capture dates of juncos in relation to date does not indicate that the bulk of early-autumn arrivals in Indiana are made up of young (data not shown). However, when we compare dates of first capture of the year among individuals caught in two different autumns (no later than December), initially as young and later as adults, we obtain the following results (Table 7). Among 41 cases, 28 juncos were caught at an earlier date when they were young than when adult (sign test, $z = 2.19$, two-tailed, $p = 0.028$). When the same comparison is made of 16 cases of birds caught in two autumns in ***both*** of which they were adult, the date in the first year was earlier in eight instances and later in the other eight. Further, in both the sample of 41 and the sample of 16, the median and mean first dates for the capture of young were at least one week earlier than the median and the mean first dates for adults (Table 7). These results are consistent with our data showing earlier onset and termination of zugunruhe in young, and priority in arrival time may play an important

Table 7

Initial capture dates[a] of juncos[b] caught in Indiana during more than one autumn, according to age in autumn of first capture.

	Date of First Capture			
	Autumn of first capture		Autumn of subsequent capture[c]	
Age in autumn of first capture	mdn	$\bar{x}$	mdn	$\bar{x}$
Young (n = 41)	24 Nov	25 Nov	3 Dec	2 Dec
Adult (n = 16)	18 Dec	10 Dec	17 Dec	12 Dec

a = Only individuals caught for the first time no later than December in both the first and later year are included.

b = Both males and females are included.

c = In a few cases the year of subsequent capture was separated from the year of first capture by a winter in which the individual was not caught at all.

role in determining the structure of winter populations. However, the results could be explained in other ways. Adults may be harder to catch than young and may escape capture for a longer time after settling in their winter quarters. Also, the rate of fidelity of juncos to winter sites is low. Therefore, site-faithful birds are not representative of the full population, and they may differ in other aspects of their migratory behavior as well, including its timing.

Whatever the significance of the age difference in the timing of autumn zugunruhe, the role of endogenous factors in determining differences in distance migrated is apparently not great. As indicated, the duration of the migratory state did not differ among classes, but there was a tendency toward greater activity per night by classes making longer migrations, and this might translate into earlier take-offs and longer flights by members of those classes. Greater activity per night might also reflect greater motivation to migrate under any particular set of weather conditions and therefore a higher probability that the individual will fly under those conditions. Collectively or alternatively, these tendencies could foster longer migrations by both females and adults, and further study of these possible mechanisms seems warranted.

Possible interpretations of the spring data are clouded by the persistence of restlessness beyond the normal dates for termination of migration (compare Figs 1 and 5). In addition, our samples were small. For either or both reasons, the differences in spring seasonal scores may be meaningless. The two tendencies in caged adults to become restless at earlier dates and to engage in more activity per night might represent, respectively, either an earlier initiation of migration or a longer migration

by free-living adults and longer flights per night. However, field evidence from Indiana has as yet revealed no earlier start of migration by adults than by young, when comparison is made of juncos known to have been members of the winter population (Ketterson and Nolan 1983a, Table 3).

CONCLUSION

Clearly, our results are inconclusive as to the importance of endogenous factors in regulating distance migrated by the junco's sex-age classes. We are reluctant to ignore the fact that in both autumn and spring the interclass variation in zugunruhe scores tended to be consistent with expectations derived from the winter distribution, even though few differences were significant. On the other hand the data are equivocal at best, and it is reasonable to think that selection may have favored exogenous regulation in the junco. Weather varies greatly and unpredictably from year to year throughout eastern North America, affecting seed production in summer and food availability in winter (Pulliam and Parker 1979). The capacity to respond flexibly to this variation would have its advantages. Rabenold and Rabenold (1985) have found that members of the non-migratory mountain race of the dark-eyed junco disperse to different elevations from year to year, depending upon winter conditions. We might therefore expect in the migratory junco the ability to abbreviate migration distance when conditions predict favorable winter foraging conditions, at least to the extent of curtailing movement after completing some initial leg(s) of the migration.

Even if interclass differences are in some measure the product of endogenous regulation, we now believe that this would be difficult to detect in the junco. Monitoring of zugunruhe yields only an imprecise measure of the underlying physiological state, and in differential migrants all individuals are, by definition, in that state. Unlike the qualitative differences that distinguish migratory categories in partially migratory species like the European robin ***Erithacus rubecula*** and probably other partial migrants (Biebach 1983), any differences among differential migrants would be quantitative. Furthermore, winter populations of juncos at all latitudes are made up of all four sex-age classes. Only the ratios differ, and this suggests considerable variance in the distance migrated by members within the same sex-age class. For these reasons, even among juncos from a single local breeding population, detection of the existence of any endogenous regulatory component and of interclass differences in that component would require larger samples than we studied.

We conclude that our data provide some support for the hypothesis that an endogenous mechanism may affect the distance juncos migrate, but it seems unlikely that it supplies migrants with sufficient information to account for the differential distribution shown in Figure 2.

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STRATEGIES OF MIGRATORY FLIGHT, ILLUSTRATED BY ARCTIC AND COMMON TERNS, *STERNA PARADISAEA* AND *STERNA HIRUNDO*

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ABSTRACT

The arctic tern is probably the most famous of all migrant birds, by merit of its amazing migrations between northern tundras and fiords, and the Antarctic pack ice zone. A short-range tracking radar has been used to record migratory flights of arctic and common terns across land, mainly during late July in Sweden. The terns climb to cruising altitudes 1000 to 3000 m above sea level and probably even higher. Their average rate of ascent of + 1.2 $m \cdot s^{-1}$ in compact flock formations is possibly determined by a balance between the benefit of quickly reaching higher altitudes with relatively favorable winds and the cost of a reduced horizontal distance covered during the ascending phase. In level flight across land the terns fly faster than predicted by aerodynamic models. Such a rapid flight speed may be preferable if the time saved facilitates efficient restoration of energy reserves at the destination. The terns appear to travel on fixed headings without compensating for wind drift. As strong headwinds increase with altitude, they abort their overland departure and return to migrate at lower altitudes over the sea along coastlines. At marine resting places the terns store large amounts of fat; arctic terns may complete their migratory journey in four or five long-distance flights which sometimes extend over continental areas. Migratory expenditures may account for almost one quarter of the total energy budget in this species, being considerably more than the energy expenditure for breeding and molt.

INTRODUCTION

Along with the Adèlie penguin ***Pygoscelis adeliae***, Antarctic petrel ***Thalassoica antarctica***, and snow petrel ***Pagodroma nivea***, the arctic tern ***Sterna paradisaea*** is one of the dominant bird species in the Antarctic pack ice environment during the austral summer (Salomonsen 1967a; Cline, Siniff and Erickson 1969; Parmelee 1977; Zink 1981a,b). After a migratory flight of nearly 20,000 kilometers from their northern breeding grounds, the arctic terns stay in Antarctica for about three months from December to March to forage and fatten on krill (euphausiids) and to undergo a rapid molt; molting seriously hampers the terns' flight capability, requiring them to land frequently on the ice. The common tern ***Sterna hirundo*** is slightly larger than

the arctic tern and, during the nonbreeding season, lives on small fish caught in coastal waters rather than on offshore plankton as does the arctic tern. The common terns, which breed on the Great Lakes and the interior of North America, winter on the Gulf of Mexico and the Pacific coast of Central America and northern South America, while common terns which breed in coastal New England migrate across the western Atlantic Ocean to the West Indies and northeastern South America (Austin 1953). Common terns breeding in the North Sea region winter mainly along the coast of tropical west Africa, while Scandinavian terns, especially those from Finland, extend their journey up to 15,000 km to South African waters (Glutz von Blotzheim and Bauer 1982). The loss and replacement of primaries occurs slowly and successively on the nonbreeding grounds thereby enabling the terns to maintain an efficient flight capability throughout the protracted molting period.

Arctic and common terns have light-weight and long slender wings designed for energy-saving flight at low speeds, including hovering (a fat-free mass at 0.11 kg and a wing span at 0.8 m are characteristic of both species—the common tern is on average about 10% heavier than the arctic tern, although there is considerable individual variation; cf. Glutz von Blotzheim and Bauer 1982, Brough 1983 and J. Rayner, unpublished). The estimated power curve (power in relation to flight velocity) for the above-mentioned mass and wing span (Pennycuick 1975) is shown in Figure 1. According to Pennycuick's flight mechanics model, the flight speed associated with the minimum cost of transport, V_{mr}, with no/neutral winds is estimated to be about 9.7 $m \cdot s^{-1}$ at sea-level (about 10.2 $m \cdot s^{-1}$ at 1000 m above sea level according to the power curve calculated in Fig 1). That common terns fly slowly is substantiated by various field observations which give estimates of flight speed ranging from 6 to 13 $m \cdot s^{-1}$ (Glutz von Blotzheim and Bauer 1982) with typical mean values of 11 $m \cdot s^{-1}$ (Austin 1953) and 10 $m \cdot s^{-1}$ (Hatch 1975). The most accurate velocity measurements have been made by Doppler radar for common terns on feeding flights to and from their breeding colonies and give average speeds of 11.6 $m \cdot s^{-1}$ (Schnell 1965) and 9.1 $m \cdot s^{-1}$ (Schnell and Hellack 1979) under calm wind conditions.

Adaptations for migration include flight speed and behavior in relation to wind, altitude, thermals, fat load, flocking, etc., (cf. the fifteen testable predictions about adaptations in bird flight by Pennycuick 1978). Furthermore, the birds' choice of flight direction and route in different winds, and their choice of departure time and weather conditions are also important components of their migratory strategy (Alerstam 1981). I will try to illustrate some of these aspects of the flight behavior of the arctic and common terns based on radar and field observations of tern migration in Sweden.

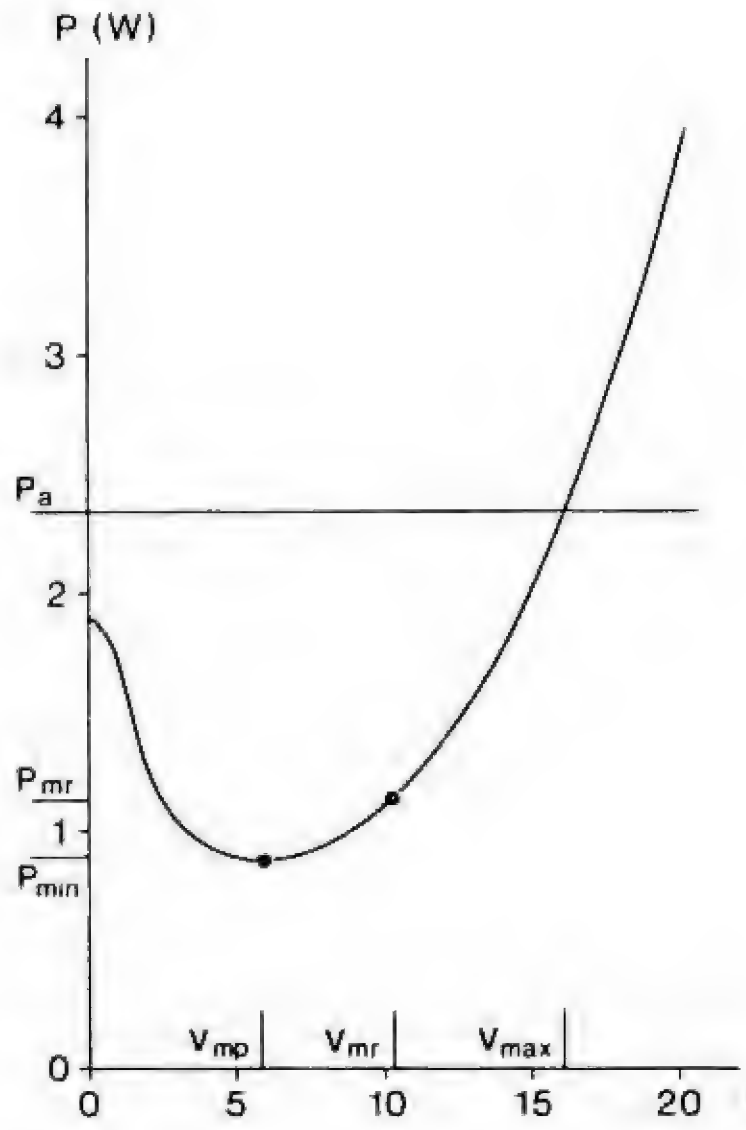


Figure 1

Flight power P (watts) in relation to air speed V_a($m \cdot s^{-1}$g), estimated for the arctic and common terns (mass = 0.11 kg, wing span = 0.8 m, air density 1.11 $kg \cdot m^{-3}$g corresponding to approximately 1000 m above sea level, Pennycuick 1975). The total mechanical power divided by the mechanical efficiency yields the corresponding chemical power input. Hovering power (V_a = 0g) represents a rough estimate. The power curve is U-shaped with a minimum P_{min} g at flight speed V_{mp} g (mp = minimum power). Under calm conditions the tangent from the origin to the power curve,

$$\frac{dP}{dV_a} = \frac{P}{V_a}\ \text{g},$$

defines the point of minimum cost of transport,

$$\frac{P_{mr}}{V_{mr}}\ \text{g},$$

for which the maximum range is achieved on a given amount of energy. (V_{mr} g is decreasing with tailwinds and increasing with headwinds according to the condition,

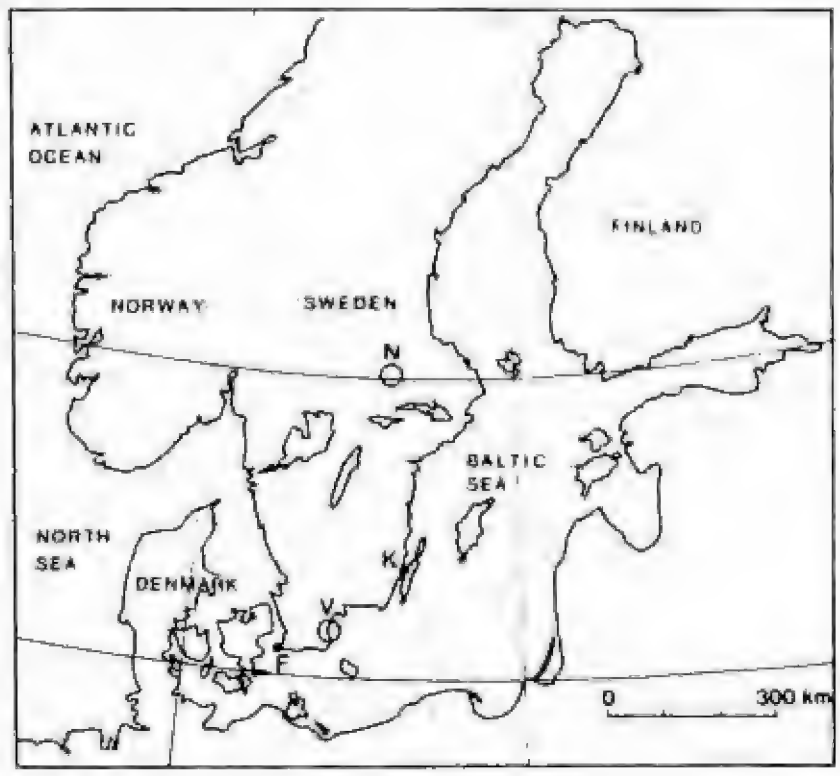
$$\frac{dP}{dV_a} = \frac{P}{V_g}\ \text{g},$$

where V_g denotes the ground speed, cf. Pennycuick 1978). The maximum power continuously available to the terns, P_a g, as limited by their muscular capacity (cf. Weis-Fogh and Alexander 1977), is tentatively calculated from radar records of terns (Table 1) climbing for more than ten minutes at climbing rates $V_z > 1.1$ $m \cdot s^{-1}$g (mean for seven flocks $V_z = +1.2$ $m \cdot s^{-1}$, $V_a = 9.5$ $m \cdot s^{-1}$g), assuming that these terns were flying at maximum sustained power. P_a g calculated in this way, indicates that the terns are capable of continuous hovering in calm weather (as also concluded by Rayner 1979) and that their maximum air speed in horizontal flight V_{max} g is about 16 $m \cdot s^{-1}$.

FLIGHT BEHAVIOR

Radar and Field Observations

Tern migration proceeds both along the coastlines and across the mainland of Sweden. Because arctic and common terns are difficult to distinguish in the field (from a distance they are often impossible to tell apart), and their migratory flight behavior is probably more or less the same, they are treated together in the following account of radar and field observations. That both species are involved in the movements discussed herein has been confirmed at all sites, but proportions remain uncertain.



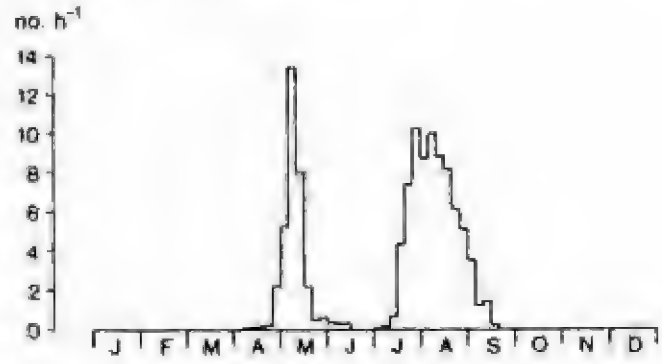


Figure 2

Sites of radar (circles) and field observations of tern migration. Arrows indicate concentrations of migrating terns at the south Baltic coast and at Lake Vänern (cf. text). The graph at the bottom shows the seasonal pattern of arctic/common tern migration in southern Sweden on the basis of field counts conducted by Ottenby Bird Station at Kalmarsound (site K) from 1958–1972. The average number of migrating terns (northwards in April–June and southwards in July–September) is calculated for five-day periods including all days with more than four hours of observation.

Field counts at Kalmarsound (K in Fig 2), where a few thousand arctic and common terns pass northward through the sound in spring and southward in the autumn, form the basis of the seasonal migration pattern shown in Figure 2. During the autumn migration at Falsterbo (F) the terns fly almost due W, or even WNW, and arrive along the southern coast of Scania. Large concentrations of autumn-migrating terns have been reported along the southern Baltic coast (Neubauer 1979) and at the southwesternmost bay of Lake Vänern in western Sweden where 16,000 terns were counted during July–September 1982 ascending over land towards the west coast of Sweden (Johansson 1982).

Ringing recoveries show that baltic terns leave on a broad front across the Scandinavian peninsula, common terns migrate mainly towards the North Sea coast, and to a large extent arctic terns also migrate across central and northern Scandinavia towards the Atlantic Ocean off Norway (Saurola 1978). The latter route involves the crossing of 450–700 km of land over the Scandinavian mountains which average about 1500 m above sea level.

Migratory flights of terns were monitored by a small tracking radar at Vitemölla (V in Fig 2) in July and September 1982 and at Norberg (N) in July 1983. The former site is located at a gently curving bay on the east coast of Scania, where large numbers of migrating terns depart inland in a westerly direction traversing Scania and Denmark in a direct flight from the Baltic to the North Sea, a distance of about 380 km. The Norberg site is dominated by coniferous woodland with many small lakes (situated at a strong magnetic anomaly).

Data about the range, elevation and bearing of the target were read by computer (HP-85) every ten seconds from the radar which was operated in automatic tracking mode. Position, altitude, flight direction and velocity were calculated and plotted. Hydrogen balloons with reflectors of aluminum foil were released and tracked by radar to obtain wind velocity data at different altitudes. Wind direction and speed were averaged over 30-sec tracking intervals which corresponded to altitude strata of about 75 m. Heading and air speed of bird flocks were calculated from wind data at the altitude stratum in which the birds were flying. Hence mean air speed for a flock ascending or descending through a series of altitude/wind strata is the average of successive calculations for each such stratum traversed by the birds. Winds were measured at frequent intervals within an hour before or after radar registration of a bird target. For the tern data presented in this paper, winds were measured 14–62 min before or after the radar registrations of the birds, with a median time difference of 36 min.

The maximum range of the radar (3 cm wavelength, 40 kW peak power, pulse duration 0.3 μs, pulse rep. frequency 1800 Hz, antenna diameter 1 m, pencil beam) for tracking birds is 4–15 km, depending on the size of the bird(s) flocks and their angle of aspect. Accuracy of the estimated position is usually within ± 25 m. The radar is equipped with 9× and 18× binoculars which permit the two operators to identify the targets and report the birds' flight behavior to a tape recorder simultaneously with the computer registrations.

Table 1

Radar registrations of arctic/common tern flocks migrating across land in Sweden. Tern flocks were tracked by radar in the period from four hours before sunset until half an hour after sunset (number of terns in the latest flock could not be definitely established because of the dusk and high altitude). The overall speed of climb or descent, V_z, and ground speed V_g is given for each flock together with the mean air speed V_a (based on calculations for different wind/altitude strata as described in the text; all speeds in $m \cdot s^{-1}$). A few brief intervals of circling flight were excluded from speed calculations and are listed in Table 2.

Radar site	Date	Time ± sunset	Flock size	Duration	Height (m asl) from	to	V_z	V_g	V_a
V (30 m asl)									
1	18 July	+ 18m	2	11m	188	786	+0.91	8.3	9.5
2	19	−1h 11m	12	14m 10s	730	1697	+1.14	10.0	10.5
3	20	−2h 28m	12	17m 50s	133	1517	+1.29	5.5	8.7
4		−1h 37m	5	13m 50s	742	1660	+1.11	8.3	8.6
5	22	− 04m	2	2m 40s	2618	2818	+1.25	15.6	11.1
6	23	− 14m	7	13m 20s	2051	2565	+0.64	8.2	9.9
7	26	−3h 04m	25	24m 40s	64	1831	+1.19 (+1.15*)	6.9*	10.9*
8		− 19m	3	8m 30s	74	693	+1.21	10.8	8.9
9	27	−4h 00m	7	5m 40s	101	519	+1.23 (+0.81*)	11.8*	9.7*
10		−3h 38m	15	11m	58	453	+0.60 (+0.27*)	13.1*	10.6*
11	28	+ 19m	2	8m 10s	546	1284	+1.51	9.8	9.0
12	29	−2h 49m	26	16m 30s	104	1411	+1.32	11.0	9.9
13		− 26m	4	10m 50s	768	1579	+1.25	12.0	8.2
14		+ 30m	?	5m	1684	1991	+1.02	14.2	10.0
15	30	−2h 52m	21	27m	92	1809	+1.06 (+1.00*)	9.5*	10.6*
16		−1h 31m	21	18m 40s	467	1793	+1.18	8.6	10.0
17a	11 Sept	+ 15m	6	9m 10s	970	1574	+1.10	5.6	12.5
17b				5m 30s	1574	883	−2.09	10.0	16.0
18	12	− 21m	12	14m 30s	328	991	+0.76	7.0	12.0
N (185 m asl)									
19	21 July	−3h 01m	2	3m	1762	1769	+0.04	12.0	15.1
20		−2h 55m	7	2m	2088	2118	+0.25	12.0	12.6
21		−1h 41m	9	2m 40s	1390	1220	−1.06	18.3	16.9
22	22	− 25m	2	4m 30s	1419	1391	−0.10	17.6	13.9

* excluding circling in thermals

Radar registrations of migrating tern flocks (all visually identified) are listed in Table 1 and comprise 22 different flocks continuously tracked during a total time of 4 h and 10 min. To a large extent the terns depart across land in the afternoon and evening, completing the main part of their flights at night. At coastal sites, like Ottenby and Falsterbo, tern migration may be observed at all times of the day, but distinct peaks usually occur early in the morning shortly after sunrise and in the evening before and at sunset (Edelstam 1972; G. Roos, unpublished).

Terns registered at site V were ascending inland in a WSW direction in compact flock formations, often vee or echelon. All but two of the flocks were still climbing when radar tracking was discontinued. One of the two exceptions was flock 17 which climbed into increasing headwinds up to 1600 m above sea level, after which the terns descended rapidly and returned towards the Baltic Sea (cf. below and Figs 10 and 11). The other was flock 18 which faced a similar although not quite so unfavorable wind situation. Headwinds increased from 4−5 $m \cdot s^{-1}$ in the altitude interval 300−800 m above sea level, to 10 $m \cdot s^{-1}$ at 1400 m above sea level. The terns stopped their climb at 1000 m above sea level (with a headwind at 7 $m \cdot s^{-1}$) and continued inland on level flight for the final three and a half minutes of this radar registration.

At site V, terns arrived at low altitude in scattered parties over the sea along the shoreline. They flew in a slow easy-going style, sometimes swooping towards the water's surface, or diving and catching fish as they went. Juveniles would occasionally alight on the water surface to be fed by adults. At the innermost part of the bay, their flight behavior changed drastically as they began climbing inland. Their flight became intent, with continuous and vigorous deep wing beats, and the birds aggregated into flock formations (large flocks could be divided into interchanging formation groups). Sometimes the terns started their climb far offshore as indicated by flocks which pass the shoreline at site V at altitudes from about 1000 m (flocks 2, 11, 13) to 1800 m (flock 14) or even 2300 m (flocks 5, 6). The latter two flocks probably started to climb at least 20 km offshore.

The terns passing overhead at site N flew in a jerking manner, with a reduced wingstroke amplitude and wings flexed backwards (reduced wing span), a flight style obviously adapted for relatively rapid flight. The birds were spaced some distance apart in the flocks and were not flying in formation, except in flock 22, where the two birds arrived in rather close pair formation. However, they suddenly banked, dove rapidly and separated completely, one of them disappearing far below the other (continued to be tracked by the radar). This reaction, as well as the unexpected descent by flock 21, is possibly related to the strong anomalous geomagnetic conditions in the area (to be evaluated elsewhere).

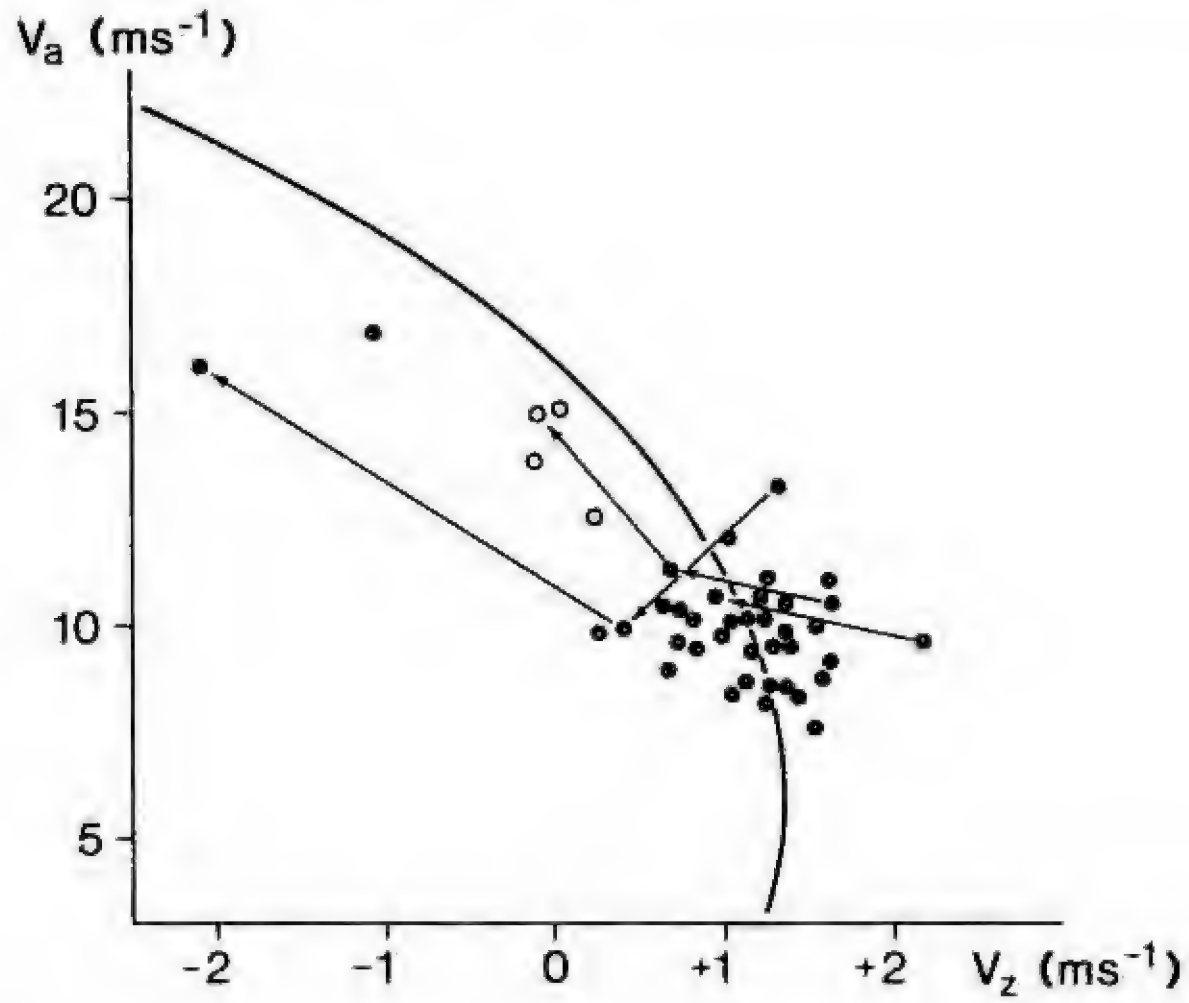


Figure 3

Mean air speed V_a in relation to vertical speed V_z in arctic/common terns (42 sequenes of a uniform V_z in 22 tern flocks, cf. Table 1). Open symbols denote flocks in level flight. The line shows the upper speed limit for terns flying at maximum sustained flight P_s, calculated according to the theoretical power curve and estimated P_s in Fig 1. The highest rate of climb recorded, +2.18 m·s^{-1}, was achieved by flock 15 during two minutes, soon after two flock fractions had merged in active circling flight (Table 2), and all birds together headed inland in a very compact flock formation. After this spell of exceptional climb rate, the flock changed to a rate of climb about +0.95 m·s^{-1}, steadily maintained for at least twelve minutes (indicated by arrow). The climbing sequences of flocks 17 and 18 are also indicated by arrows. Flock 17 achieved an exceptional air speed of 13.3 m·s^{-1} during at least seven minutes full climb (+1.31 m·s^{-1}) into very strong headwinds, whereafter the birds slowed down (exhausted ?) for two minutes and finally descended rapidly in return flight (cf. Fig 10 and 11). Flock 18 climbed steadily at +1.64 m·s^{-1} during four minutes, reduced V_z to +0.65 m·s^{-1} during the following seven minutes, before assuming level flight.

Flight Speed and Climb Rate

Changes in ascent rate by the terns were often relatively abrupt, between which they flew with a uniform rate of ascent. Such intervals of uniform ascent rate, of 2 min to over 12 min in duration, were distinguished, and mean air speed is plotted in relation to vertical speed in Figure 3. As expected, the air speed is highest for descending terns (flocks 17b and 21), 16.0−16.9 m·s^{-1}, intermediate for flocks in level flight (flocks 19, 20, 22 and final sequence of flock 18), 12.6−15.1 m·s^{-1}, and lowest for the climbing flocks. The overall means and standard deviations for 36 climbing sequences were: $V_a = 9.9 \pm 1.1$ m·s^{-1} ,$V_z = 1.2 \pm 0.4$ m·s^{-1}.

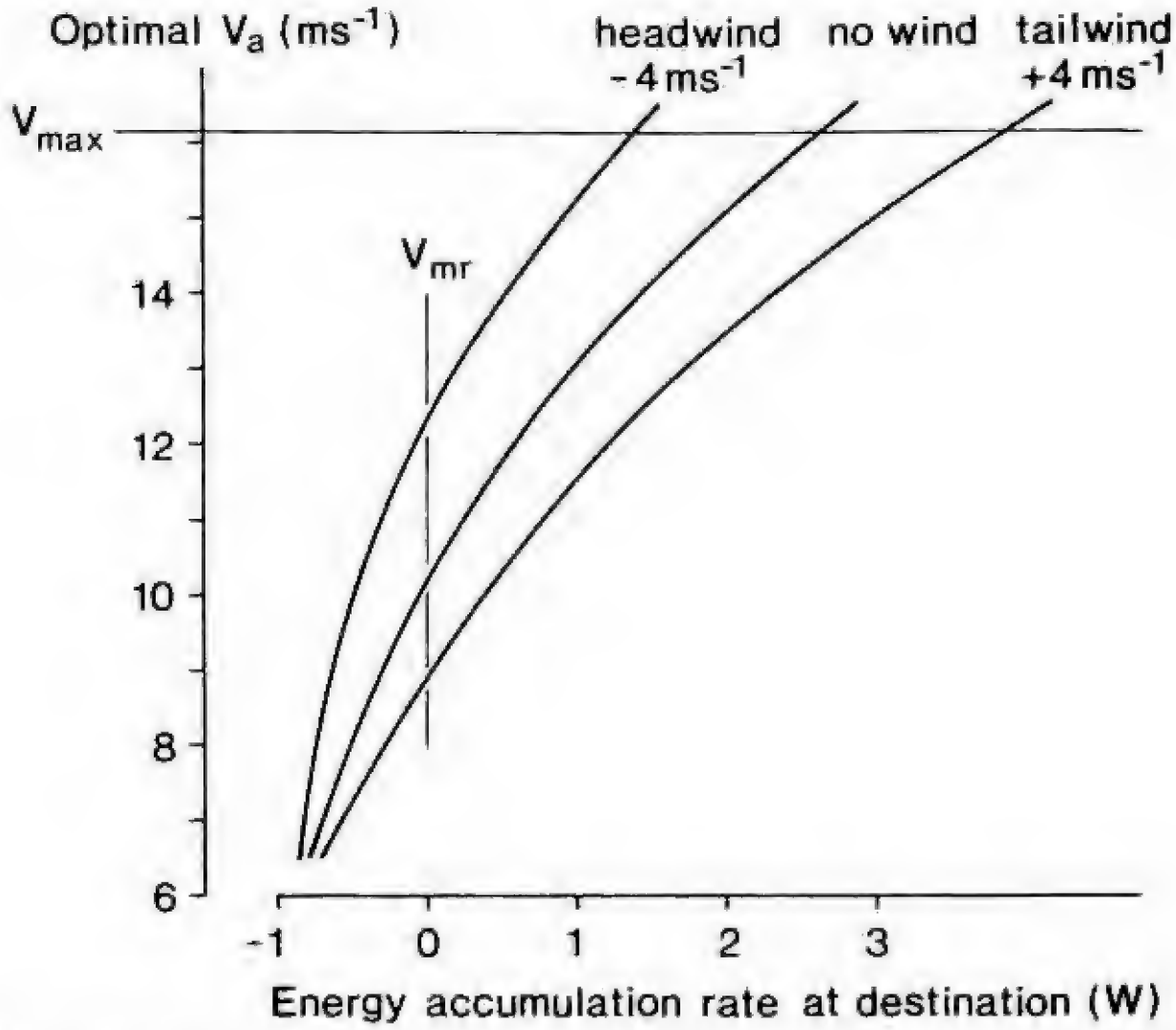


Figure 4

Optimal air speed V_a for arctic/common terns in relation to energy accumulation rate (given as the equivalent mechanics power) upon arrival at the destination. Calculations have been made for different wind conditions according to the condition

$$\frac{dP}{dV_a} = \frac{P + E}{V_g}$$

(cf. Fig 1) where E = energy accumulation rate. An energy accumulation rate equivalent to 1 watt of mechanical power corresponds to the storage of about 0.4 g of fat per hour or a daily increase of mass due to fat storage in the terns of about 4% (about 12 h of day-time feeding and fat accumulation). This estimate is probably not unrealistic at rich feeding waters.

The terns in level flight were traveling faster than the predicted V_{mr}, and also faster than terns flying at low altitude over the sea, or at their breeding colonies (cf. Fig 1 and speed measurements reported by various sources mentioned above). One possible explanation may be that terns on high-altitude overland flight increase their air speed in order to arrive more quickly at the sea, where they can efficiently restore their energy reserves. By increasing their speed $> V_{mr}$, their flight will expend more energy, but this may still be the most favorable option, provided they can more than compensate for this extra cost by foraging at their destination. The faster the rate of energy accumulation at their destination, the greater will be the optimal flight speed. With the prospects of energy loss upon arrival at the destination, e.g., a nighttime arrival with no foraging possibilities, or in cold weather, the optimal flight speed will be $< V_{mr}$. The predicted relationship between the optimal flight speed and the energy accumulation rate upon arrival at the destination is given in Figure 4. This is the same type of argument as used by Norberg (1981) who predicted optimal flight speeds in birds when feeding young.

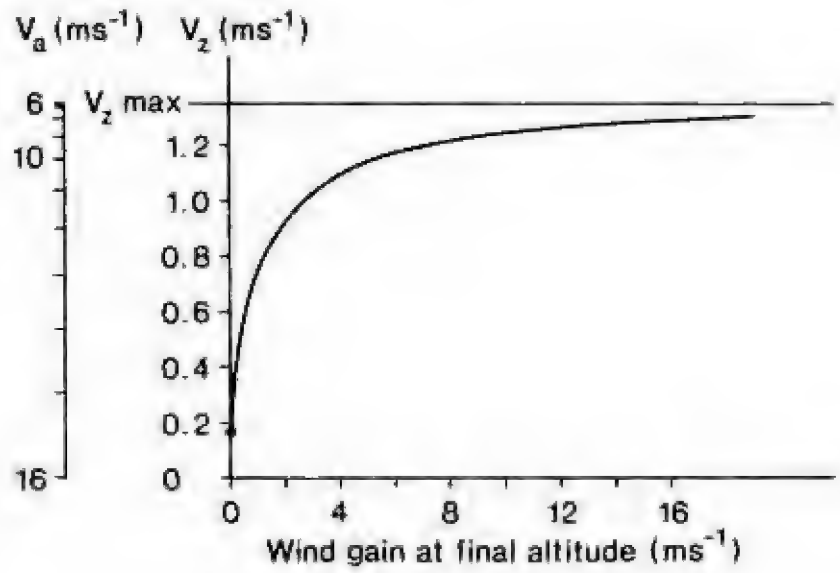


Figure 5

Optimal climbing rate in arctic/common terns in relation to wind gain at the cruising altitude relative to that at lower altitudes (W). It is assumed that the birds climb at maximum sustained flight power P_a. Calculations are based on the theoretical power curve and the estimated P_a in Figure 1, according to the condition:

$$\frac{dV_z}{dV_a} = \frac{V_z}{V_a - V_{max} - W.}$$

Of course, there are other possible advantages associated with a high air speed $> V_{mr}$ that may offset the extra energy costs, such as competitive dominance at the destination or a reduced risk of wind drift during the flight journey.

Furthermore, one should be aware that the predicted V_{mr} (and V_{mp}) may be inaccurate due to imperfections in the present flight mechanics theory for birds which is based upon preliminary approximations adopted from aircraft aerodynamics.

For the climbing terns, there was no significant correlation between V_a and V_z ($r = -0.14$, 36 climbing sequences shown in Fig 3). However, V_a was significantly correlated with both altitude ($r = +0.34$, $p < 0.05$) and wind speed, as measured by the variable $W = V_g - V_a$ ($r = -0.34$, $p < 0.05$), although not with flock size ($r = +0.29$, ns, $n = 17$ climbing tern flocks). The linear multiple regression equation of V_a in climbing terns in relation to these variables was $V_a = 8.8 + 0.8\,H - 0.15\,W$ (H = mean altitude in km, $R = 0.55$, $n = 36$ climbing sequences). Similar calculations for V_z revealed a statistically significant effect of altitude only ($r = -0.40$, $p < 0.05$, $n = 36$) according to the equation $V_z = 1.4 - 0.25\,H$. That the rate of climb usually became reduced with increasing altitude was also indicated by changes in climb rate observed in the flocks at site V (excluding flock 17 and the level flight of flock 18). Out of 19 changes in climb rate with increasing altitude, climb rate increased in only 5 but decreased in 14 instances ($p = 0.03$).

The maximum rate of climb is achieved by terns flying at V_{mp} air speed of about 5.8 m·s^{-1} according to the theoretical prediction (Fig 1). However, observed air speeds of the climbing terns were faster, averaging close to 10 m·s^{-1}. What is the optimal rate of climb, and the associated air speed? Assuming that climbing terns fly with the maximum sustained power (P_a) to reach a cruising altitude with a mean

Table 2
Radar registrations of circling flight in thermals by arctic/common terns

Flock Number	Position	Height (asl) from	to	Duration (seconds)	V_z	Circling Behavior
7	1.2 km inland	141	301	80	+2.00	Flapping flight, soaring
9	0.8 km inland	132	463	220	+1.50	Soaring, some flapping flight
10	2.0 km inland	142	495	250	+1.41	Soaring, some flapping flight
15	shoreline	92	163	70	+1.01	Flapping flight, some soaring
	0.4 km offshore	134	276	200	+0.71	Soaring
	0.9 km inland	496	688	80	+2.40	Flapping flight

expected wind gain, + W, relative to conditions at lower altitudes, their optimal climbing rate is calculated in Figure 5. By climbing steeply they will quickly reach their cruising altitude at the cost of a reduced horizontal distance covered. A steep climb is favorable if wind gain provides a sufficient cruising speed (V_{max} + W) in the climbing time saved to more than compensate for the horizontal distance lost during the climbing phase. The more favorable the upper winds are in relation to the winds at lower altitudes, the steeper will be the optimal climb rate. For the climbing flocks at site V, the relative wind gain at the most favorable altitude between 1500 and 4000 m asl ranges from about $-3\ m{\cdot}s^{-1}$ to $+7\ m{\cdot}s^{-1}$ with a mean about $+3\ m{\cdot}s^{-1}$, according to rough estimates. According to Figure 5, this average wind gain is associated with an optimal V_z slightly above $+1\ m{\cdot}s^{-1}$, and V_a about $11\ m{\cdot}s^{-1}$, values not very different from the speeds observed in the climbing terns.

SOARING

Terns that depart inland in the afternoon when there are still rising thermal currents over land, stop to circle in thermals close to the coastline (Table 2). They circle by gliding, mixed with flapping flight, sometimes by almost pure soaring with their wings and tail fully spread. Flocks become totally disorganized and individuals circle simultaneously in different directions (like the soaring behavior in flocks of, for example, common and blackheaded gulls ***Larus canus*** and ***L. ridibundus*** and the white stork ***Ciconia ciconia***, cf. Pennycuick 1972). The final instance of circling by flock 15 was an exception, where the terns circled by vigorous flapping flight in a compact flock to join a group of terns circling overhead. Unlike many soaring birds such as gulls, raptors, storks and cranes, the terns cross land mainly at night and do

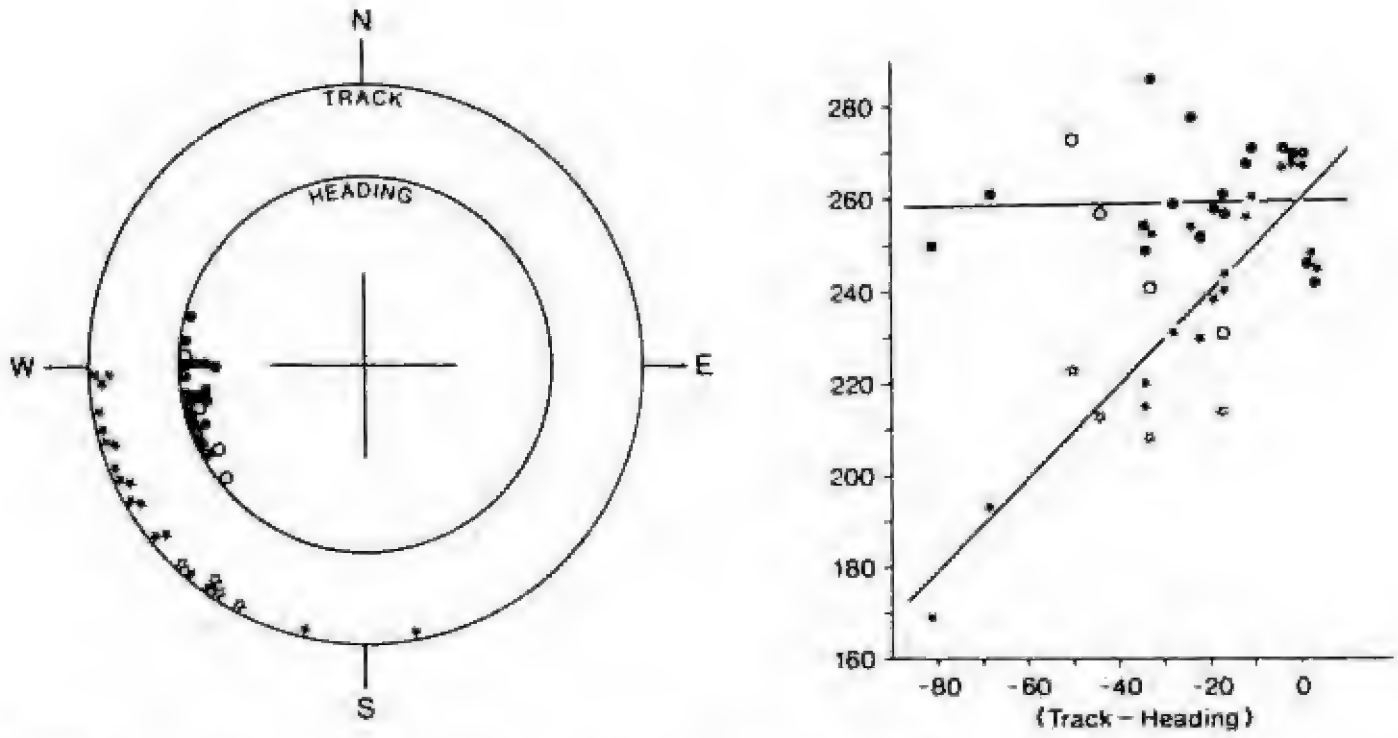


Figure 6

Track and heading directions of flocks of arctic/common terns migrating over land at sites V and N (open symbols). The mean heading is 259° (angular deviation = 13°) and the mean track is 235° (angular deviation = 25°). The graph to the right shows the heading and track directions plotted in relation to the difference between these directions, track minus heading direction. The calculated regression coefficients at 0.0 and +1.0 respectively (both with 95% confidence interval ± 0.28) indicate that there is no compensation at all for wind drift (Alerstam 1976). This conclusion holds even if the two flocks with the greatest difference between their track and heading direction are excluded, since wind speed in these cases exceeded the birds' air speed, giving regression coefficients of −0.08 and +0.92, respectively (95% confidence interval ± 0.44). However, note that, considered alone, the four flocks at site N do indicate compensation for wind drift; this may be due to chance.

not migrate by cross-country soaring but use thermals only as a temporary lift assistance to reach their desired cruising altitude. The same behavior has been noted in curlews ***Numenius arquata***, bar-tailed godwits ***Limosa lapponica***, arctic skuas ***Stercorarius parasiticus***, and cormorants ***Phalacrocorax carbo*** departing inland at site V (cf. also the occasional use of thermals by migrating European starlings ***Sturnus vulgaris***, as described by Cone 1968). By stopping to circle in thermals, the birds will lose some ground, but in return they will save energy costs for the climb.

A major part of tern migration takes place over the sea where the terns could adopt soaring flight close to the sea waves, a strategy used by many ocean birds as an economical means of flight (Wilson 1975, Pennycuick 1982). Still, field observations indicate that the terns are not likely to do this, probably because their low wing loading does not permit a fast enough gliding speed (cf. Alexander 1982). The terns normally travel by flapping flight 30−150 m from the surface (Wynne-Edwards 1935). However, in head-winds they fly close to the wave crests and many save some energy by intermittent slope soaring at the waves (field observations needed).

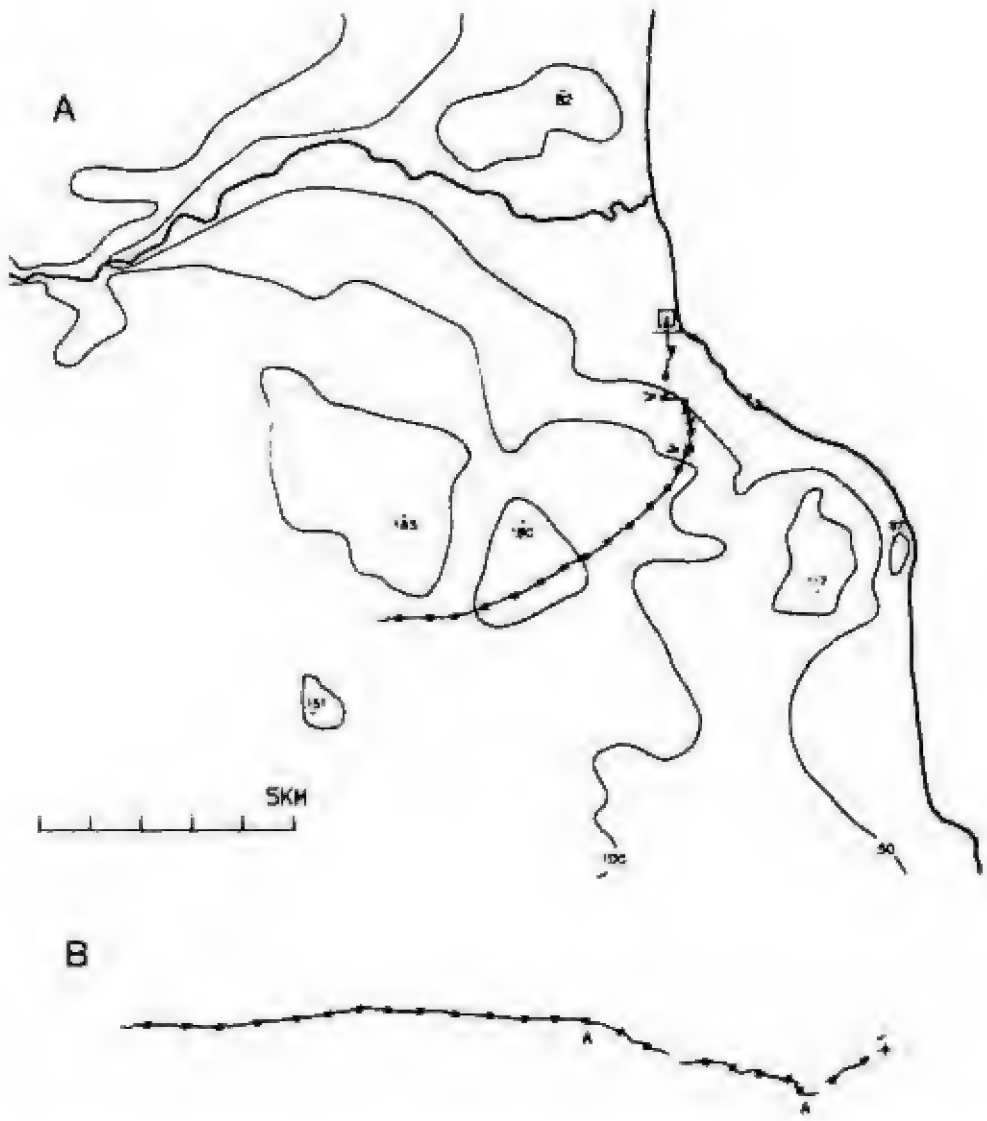


Figure 7

A. Flight route of tern flock 7 with its initial position immediately to the north of the radar station (plus sign) and curving westwards. Position is plotted in 10 sec intervals (excluding invalid radar data), with squares for each successive minute. The radar is situated at the shoreline bordering the Baltic Sea to the east, with the outflow of a small river a few kilometers to the north. 50, 100, and 150 m contour lines are indicated. B. Flight route in relation to the air ("air route"), calculated by subtracting the effect of wind from the above successive 10-sec tracking intervals. The starting point of the air route in relation to the radar station (plus sign) is the same as above. Hence the air route shows how the flight route would have appeared without wind. During the first three minutes the terns flew inland on a southwesterly heading. After a brief period of circling, with intermittent flapping flight into the wind, they headed straight into the strong WNW wind, climbing steadily but with very little forward progress. After eleven minutes, the terns reached an altitude of approximately 800 m asl. At this altitude, the headwind velocity was relatively low, and the birds adopted a constant heading almost due west (cf. Fig 8).

WIND DRIFT

Analyzing track and heading directions of the 22 tern flocks (Table 1; using the final heading directions over land at site V) as in Figure 6, indicates that the terns fly on fixed headings and do not compensate for wind drift. This is substantiated by comparing the birds' tracks and calculated headings as they climb through altitudinal strata with different winds. The flight behavior of flock 7 is illustrated in Figures 7 and 8. After eleven minutes, when the terns had climbed through the strongest headwinds, they maintained a virtually constant heading towards due west, with their track gradually approaching the same direction, as they successively climbed through

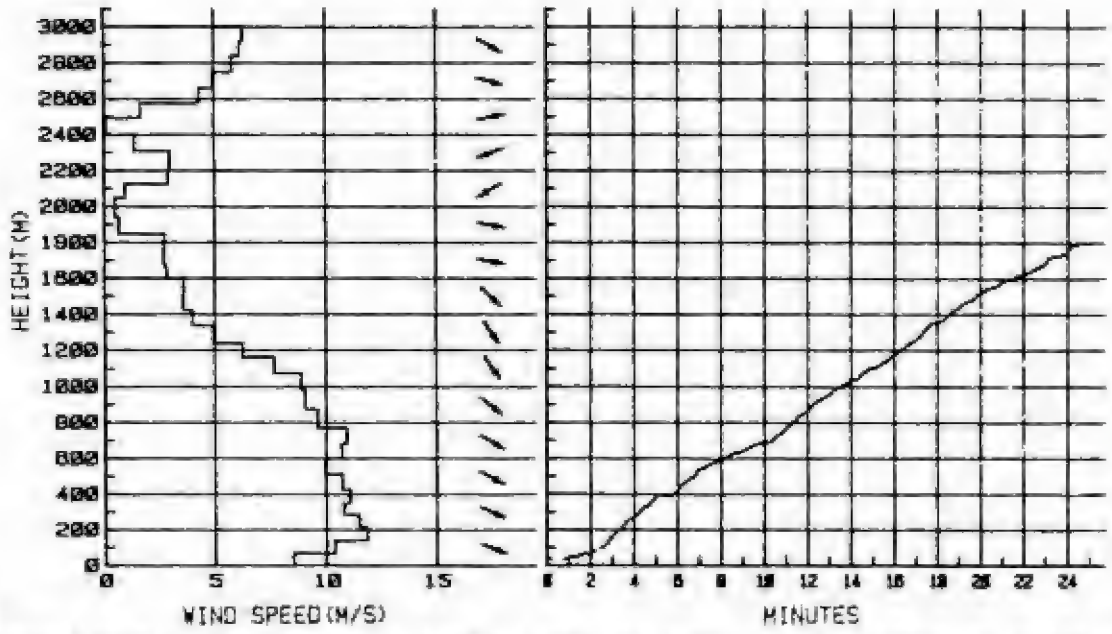


Figure 8

Altitude (above radar level) of tern flock 7 (right) and wind conditions prevailing at different altitudes (left) according to radar measurements of a hydrogen balloon. Arrows show the average wind direction in 200 m-height intervals. Note that favorable tailwinds prevail about 2200 m asl (cf. Fig 7).

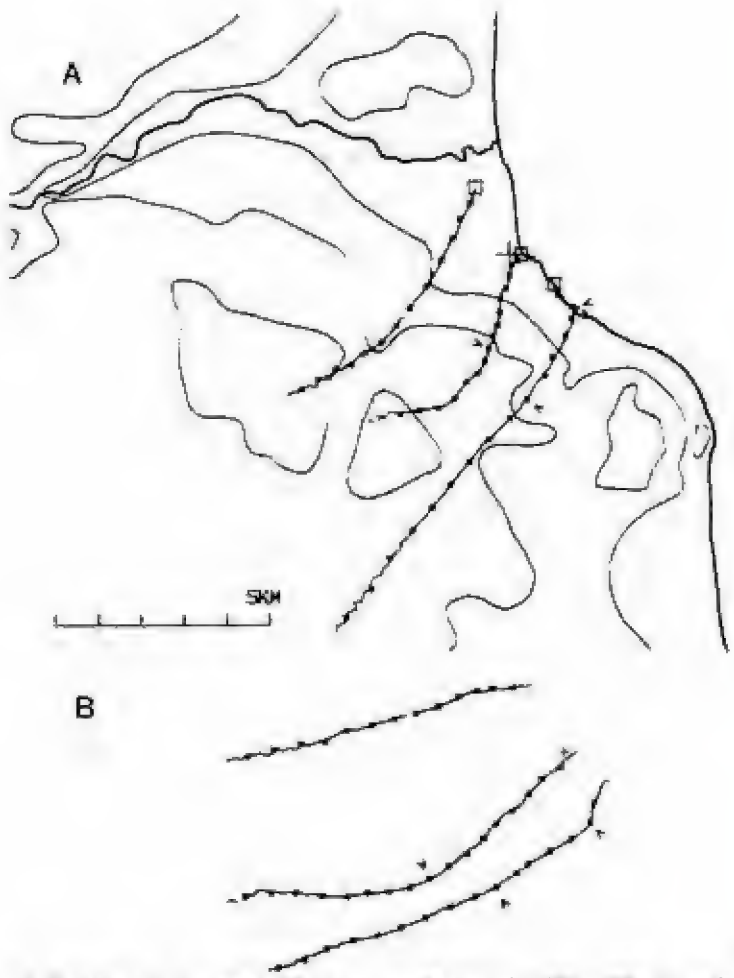


Figure 9

(A) Flight routes of flocks 4, 3, and 12 (top to bottom); (B) Their calculated "air routes." The radar site is indicated by a plus sign. Flock 4 flew on an almost constant WSW heading, with the resulting track curving as northwest winds became weaker at higher altitudes. Flock 3 initially headed SW, until after about nine minutes, and at 770 m asl it reoriented towards W and showed a flight pattern similar to flock 4. Flock 12 initially flew over the shoreline towards southeast. After two minutes and at 230 m asl, it changed heading from almost 200° to 238° and climbed inland. Five minutes later, at 690 m asl, the heading was finally adjusted to about 254° with a concomitant slight shift in the track direction.

altitudinal strata with decreasing wind speed. Similar conditions, with a relatively constant heading direction and a curving track as the birds climbed through changing winds, are illustrated for flocks 3 and 4 in Figure 9. Compensation for wind drift would be manifested by a straight track but a changing heading, as the birds encountered different winds as they climbed. However, this situation does not apply to any of the tern flocks registered. The straightest track was exhibited by flock 12 (Fig 9), but wind was rather constant throughout the altitudinal interval traversed by the birds and, consequently, so was the birds' heading.

Being far away from their final migratory destination and having no narrowly defined resting goals, an increase in the rate of their migratory progress at the cost of wind drift may be beneficial to the terns (Alerstam 1981).

Flocks crossing the shoreline at site V at low altitudes under head- or crosswinds initially flew on southwesterly headings (with resulting track directions towards S-SSW), and they did not reorient to their final constant W-WSW headings (cf. flocks 3, 7 and 12 in Figs 7–9, also flocks 1, 8, and 15) until reaching 500–800 m asl, 2–4 km inland. This did not occur in flocks crossing the shoreline at higher altitudes (> 400 m asl), as they had already established their final heading, nor did it occur in flocks climbing low over the shoreline with easterly tailwinds (flocks 9 and 10). The reason for the initial southwesterly headings is unclear; the terns may refrain from straying away from the coast until they determine if the winds are more favorable for an overland flight than a low altitude coastal flight around Scania.

FLIGHT ALTITUDE

The radar data show that the terns fly across land at altitudes of 1000–3000 m asl, and probably even higher. A possible method for locating the most favorable cruising altitude might be for the terns to ascend upon departure over land, "sampling" the winds at different altitudes as they go, and to choose the altitude where winds are found to be most beneficial. The possible rewards for climbing through altitudes with strong headwinds are evident for the case of flock 7 (Figs 7 and 8). Flocks 3 and 4 climbed past the altitude with the most favorable wind at about 1400 m asl, and flock 18 also overshot the best cruising altitude in the interval 300–900 m asl.

If headwinds prevail and increase in speed with increasing altitude, the terns will ultimately give up their attempt at overland flight, as illustrated in Figures 10 and 11. Under such unfavorable wind conditions the terns will choose to migrate at low altitude over the sea. Using the extensive fifteen-year field counts at Kalmarsound to investigate the relationship between daily intensity of tern migratory passage and weather, I found that headwinds promote low-altitude migration through this sound. In spring, tern migration was significantly associated with E and NE winds. There were no significant correlations between number of terns and wind speed, except on days with SW winds when a significant negative correlation was found (the stronger the tailwinds, the fewer terns are observed). In autumn, tern migration was primarily

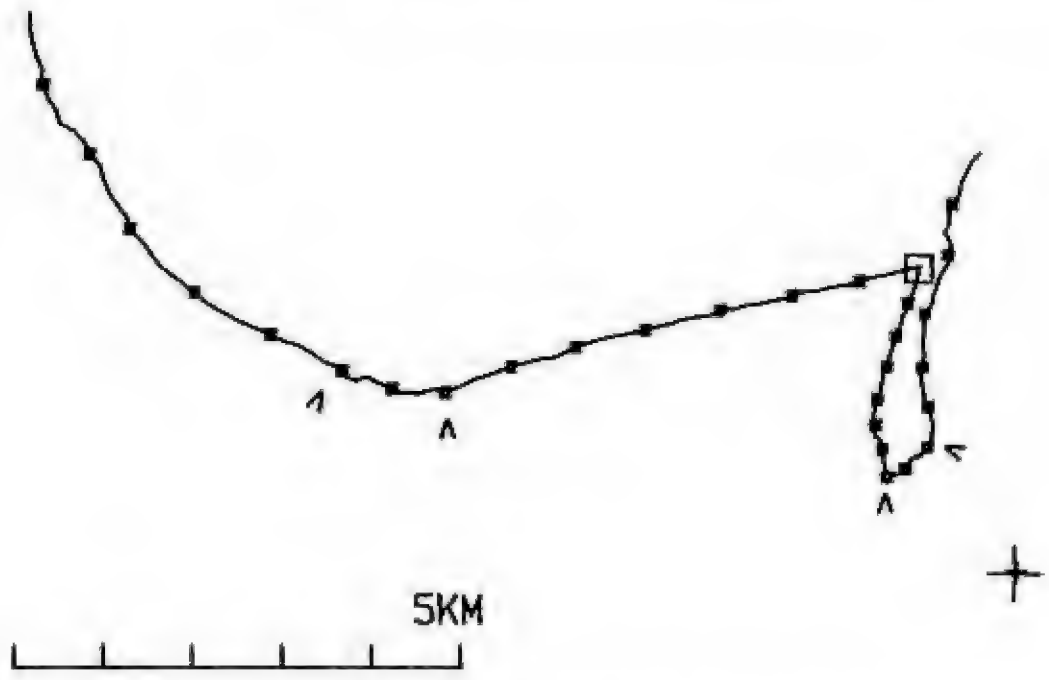


Figure 10

Flight route and calculated "air route" of flock 17. The air route (to the left) is plotted from the same initial position (large square) as the registered flight route (to the right). The radar site is indicated by a plus sign. For altitude and wind data see Figure 11. The terns were climbing on a steady WSW heading, with a resulting southward track 1–2 km inland from the coastline. Encountering strong and increasing headwinds as they climbed, they became drifted to an increasing extent, with their resulting track changing from SSW to SSE. After seven minutes, at 1520 m asl and a west wind of 13.5 $m \cdot s^{-1}$, they decreased in air speed (from 13.3 to 10.0 $m \cdot s^{-1}$) and rate of climb (from + 1.31 to + 0.40 $m \cdot s^{-1}$) for two minutes. During this time they were overpowered by the wind and carried backwards towards east and northeast. At 1600 m asl they descended steeply in a NNE return flight, with a northwesterly heading. They finally crossed the shoreline in a continued steep descent towards the surface of the sea.

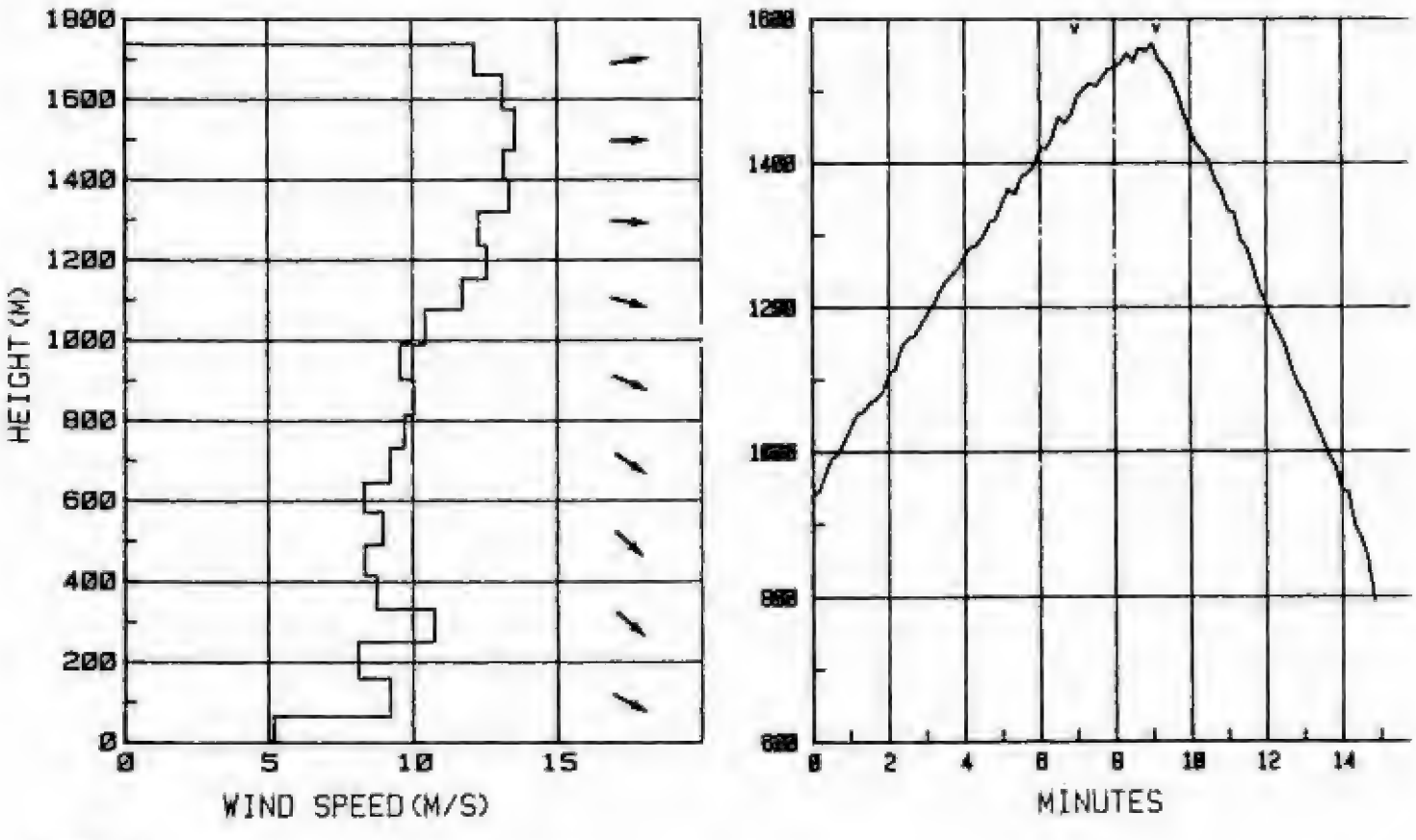


Figure 11

Altitude (above radar level) of tern flock 17 (right) and prevailing winds (left). Note that the scales of height are different for the two diagrams.

associated with SW winds At Falsterbo a correlation was also found between the number of terns migrating at low altitude and the occurence of headwinds (Fig 12). Note that some terns flew past Falsterbo into surprisingly strong headwinds. The record occurred on 27 August 1979, when 28 flocks composed of a total of 324 arctic/common terns (the second highest daily, 04−14 h, count of terns recorded in the latest ten years), were recorded heading W or WNW into a headwind of 17 $m \cdot s^{-1}$ (measured 10 m asl). The terns were able to cover ground by flying very low over the sea waves, where wind speed is reduced due to friction. However, on 22 August 1980 a WNW wind of 20 $m \cdot s^{-1}$ prevailed, and not a single tern passed by, although several were counted on the preceding and following day with WNW winds of 10−13 $m \cdot s^{-1}$ (all Falsterbo data from Gunnar Roos in litt.). Hence, a 20 $m \cdot s^{-1}$ headwind, corresponding to 10−15 $m \cdot s^{-1}$ at the sea's surface, seems to be just above the threshold for suppressing migratory flights in terns.

FLOCKING

Flying in compact flocks, particularly in formations, is probably aerodynamically efficient, thereby reducing flight energy costs (Lissaman and Shollenberger 1970, Hummel 1973, Higdon and Corrsin 1978). Terns gather into compact formations when climbing inland and to some extent in fast level flight. When some flocks of terns begin to climb inland at site V, other flocks may be seen to follow suit, sometimes gathering together into compact flocks comprising as many as 50−80 individuals. For the climbing flocks tracked by radar, there was no statistically significant difference among V_a or V_z for the nine small flocks, 2−7 individuals (mean ± s.d., $V_a = 9.7 \pm 1.3$ $m \cdot s^{-1}$, $V_z = 1.1 \pm 0.3$ $m \cdot s^{-1}$) and the eight larger ones, with 12−26 individuals ($V_a = 10.3 \pm 0.8$ $m \cdot s^{-1}$, $V_z = 1.1 \pm 0.3$ $m \cdot s^{-1}$). However, the tendency towards a somewhat higher air speed in large as compared to small flocks may be worth noting in light of Noer's (1979) finding of a positive correlation between air speed and flock size in migrating oystercatchers ***Haematopus ostralegus***, red knots ***Calidris canutus***, and dunlins ***Calidris alpina***.

FUEL ECONOMY AND ENERGY BUDGET

Upon arrival at their breeding colonies at Kandalaksha Bay, in the White Sea, the average weight of arctic terns is 110 g. Their mass gradually declines during the breeding season to about 100 g at departure time in July/August (Bianki 1977). During the fall migration, the arctic terns from Finland (Lemmetyinen 1968, Saurola 1978) and other parts of NW Europe stop at their first important staging area in the northeastern Atlantic Ocean off Norway and Britain. Here the arctic terns arrive at the peak of zooplankton abundance (Colebrook and Robinson 1961), and store fat before undertaking a rapid and direct flight to the waters off west Africa, their next refueling area. (This is indicated by a paucity of ringing recoveries from SW Europe, cf. below.) Such a direct flight of 3000−5000 km would require a fuel ratio at 30−40%

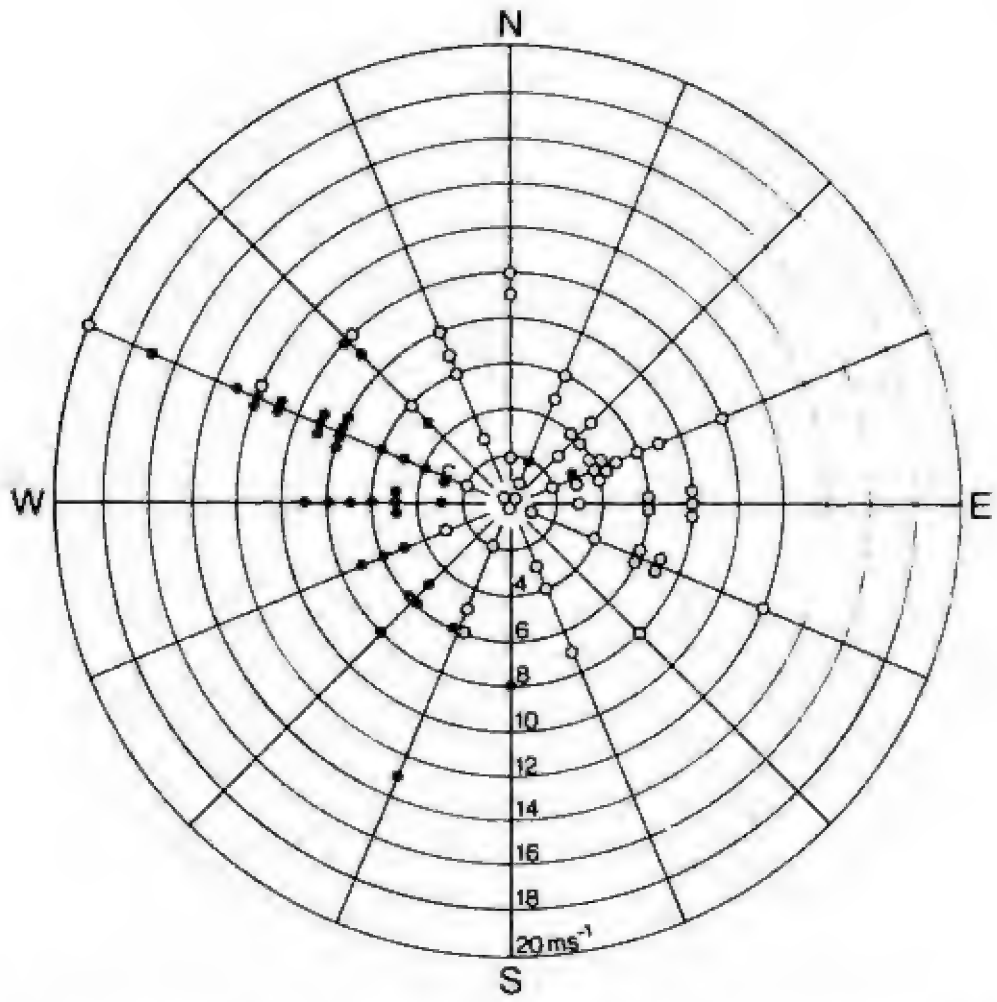


Figure 12

Daily (04−14 h) numbers of migrating arctic/common terns at Falsterbo in relation to wind direction and speed (measured at Falsterbo lighthouse, 10 m asl). Data refer to the period 11−31 Aug 1973−1982. Filled symbols indicate days with > 50 migrating terns counted (up to a maximum of 325 individuals), and open symbols indicate days when no terns were counted at all (a great number of days with 1−50 migrating terns, scattered over all wind directions, are excluded from the figure). Based on data from Gunnar Roos in litt.

(of a total body mass 0.15−0.19 kg at departure) according to flight mechanics theory (Pennycuick 1975). Terns are efficient flyers with a predicted fat consumption corresponding to about 0.4% loss in body mass per flying hour.

Arctic terns from eastern Canada and western Greenland forage pelagically in Davis Strait during August, where they become very fat (Salomonsen 1950). At the end of the month they set out on a direct flight across the north Atlantic towards western Europe, a distance of at least 3000 km, when "they stop to feed only on the rarest occasions (once seen) and never by any chance settle on the water" (Wynne-Edwards 1935).

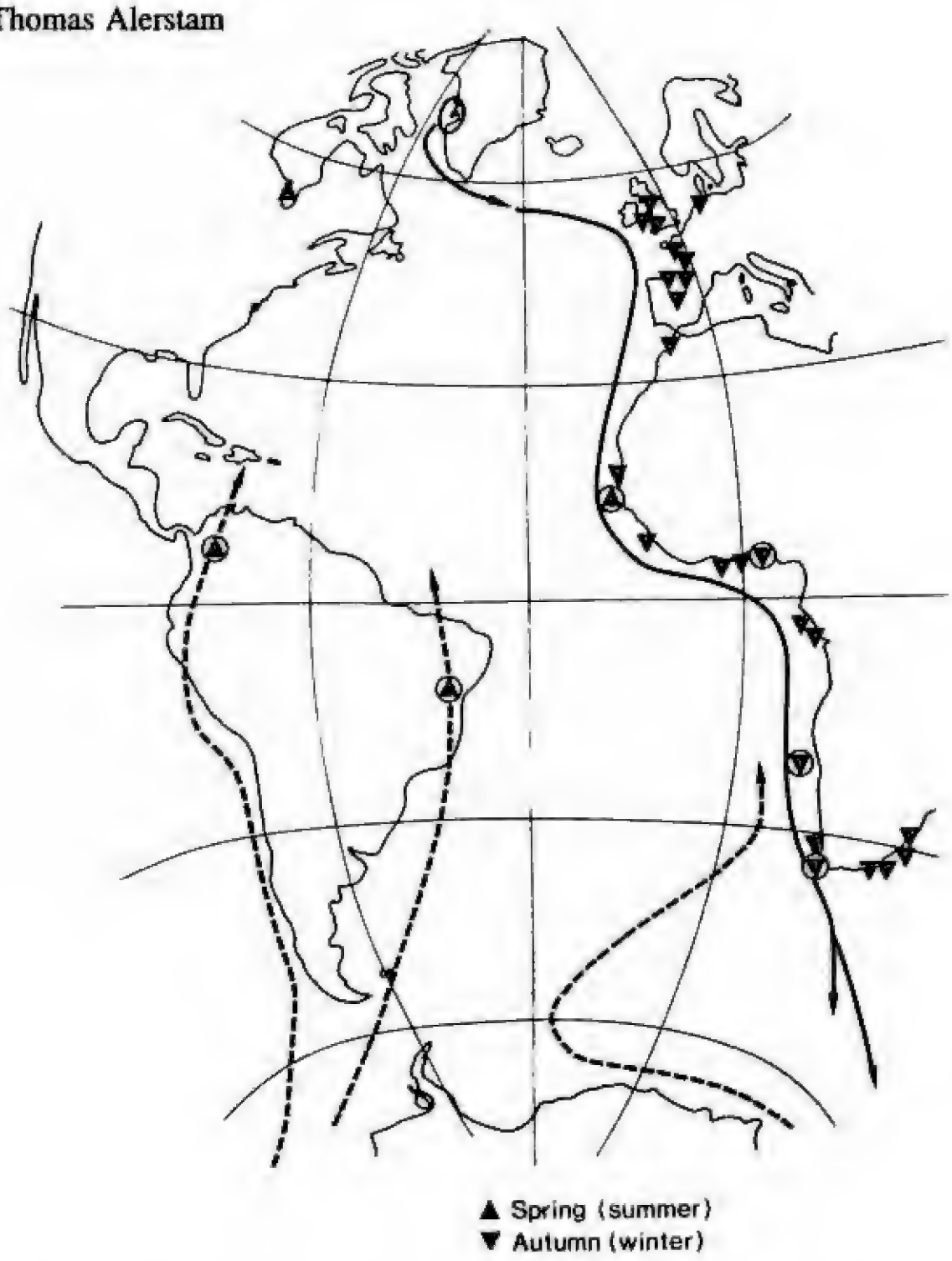


Figure 13

Recoveries of arctic terns ringed at breeding places in west Greenland (only recoveries outside Greenland are shown). Encircled recoveries refer to birds older than one year. Recoveries from Europe and west Africa are from Sept–Nov. Recoveries in Africa, dated as early as 20, 24 and 25 Sept are from Nigeria, Sierra Leone and Senegal, respectively. Two recoveries from South Africa refer to autumn migration (30 Oct and 17 Nov), while the others are dated 26 Dec–20 Jan indicating that some arctic terns, mainly juveniles, may winter in South African waters (cf. Elliott 1971). Spring recoveries come from the Colombian Andes above 2000 m asl (a ten-year old tern shot on 16 June), the Brazilian Highlands 400 km from the Atlantic coast (three-year old, reported 4 May) and from Dakar, Senegal (one and a half-year old, reported 20 March). Furthermore, a one-year old bird was shot on 4 July at James Bay in Canada (cf. Salomonsen 1967b). Ringing data were received by courtesy of the Zoological Museum, University of Copenhagen (Kaj Kampp in litt.).

The Benguela current and South African waters (Rudebeck 1957, Elliott 1971) probably constitute the final major refueling area before the arctic terns traverse the Southern Ocean towards Antarctica. Assuming that their goal is to reach the circumpolar pack ice belt, irrespective of longitude (site fidelity within the irregularly fluctuating pack ice seems unlikely), their optimal strategy should be to persistently head due south throughout the oceanic crossing and allow themselves to be drifted by the winds. Hence, the energy costs will roughly correspond to a 3000 km active flight journey in neutral winds (approximate distance from Cape Town to the pack ice at 60°S in November), even if strong westerly winds displace the terns a far greater distance over the Southern Ocean before they reach the pack ice at easterly longitudes (Salomonsen 1967a). Before their return journey across the Southern Ocean, the arctic terns store fat at their wintering waters. Although still in molt, eleven birds from the Weddell Sea in February, weighed on average 130 g, with the heaviest at 154 g (probably with fat enough for a 3000 km nonstop flight, cf. Zink 1981a).

Scandinavian common terns travel closely along the shorelines of the east Atlantic Ocean towards South Africa. Saurola (1978) compared the probabilities of autumn ringing recoveries in different countries between common and arctic terns, based on the extensive Finnish ringing data. For Norway this probability is 7.4 : 1 in favor of the arctic tern, with supplementary recoveries of arctic terns from Iceland, Shetland, and the mainland of Scotland, where there are no common terns. However, along the coasts of Holland, Belgium and France the probability is 6.3 : 1 in favor the common tern, increasing to 20 : 1 in Spain and Portugal. For west and south Africa the probability is about 3 : 1 in favor of common terns, probably mainly because of the more inaccessible and offshore flight routes of arctic as compared to common terns. Common terns store fat at the North Sea coasts in August and September, e.g., at the mouth of Elbe, where several heavy weights, in the interval 150−163 g, have been recorded (Peters 1933). This indicates that long nonstop flights, up to 3000 km or longer, are regularly undertaken not only by the arctic but also by the common tern. (Note also the flight across the west Atlantic Ocean from North to South America/West Indies by common terns, Austin 1953.)

The unprecedented one-way migration of the arctic tern may, with some wind assistance, be completed in four or five such long-distance flights. The observations of large numbers of arctic terns, not only in the pack ice at easterly longitudes but also at westerly longitudes such as the Amundsen, Bellingshausen and Weddell Seas (Parmelee 1977, Zink 1981b), may indicate that at least certain populations of arctic terns migrate around or across Antarctica, perhaps returning to the northern hemisphere by a different route from that used during the autumn. This may be reflected in the distribution of ringing recoveries of western Greenland arctic terns (Fig 13), where all autumn recoveries occur along the eastern Atlantic route, while two spring recoveries come from South America (plus one spring recovery from Senegal and one tern recovered during its first summer at James Bay). These two South American recoveries are particularly remarkable because they originate from areas far inland from the coast, one of them from high up in the Colombian Andes. The radar

observations described above show that the terns are readily prepared for high-altitude flights across land, and it may turn out that their long-distance flights, more often than heretofore suspected, extend across continental areas (cf. also recoveries of White Sea arctic terns from Ukraine and the Ural River, Bianki 1977).

The cost of transport for an arctic tern is at least 500 joules (J) of net energy input per kilometer of active flight (Fig 1 and Pennycuick 1975). With a total annual migratory journey extending over 40,000 km, the flight cost will be 20,000 kJ. With an additional cost of about 50% involved in the process of fat accumulation (Kendeigh, Dolnik and Gavrilov 1977), the total annual energy expenditure for migration in the arctic tern may be estimated at about 30,000 kJ. This is to be compared with the other major costs in the annual energy budget (very roughly estimated according to Kendeigh et al. 1977), 9000 kJ for breeding and feeding the young, 3000 kJ for molt, and probably nearly 100,000 kJ for free-living existence because of extensive flying (cf. Utter and LeFebvre 1973). Of the total annual energy budget, at most a quarter is expended at the northern breeding places (costs for breeding and 2–3 months of living), while the rest is associated with the roaming marine life of the arctic tern. This is a telling illustration of the surplus of survival resources, a rich food supply and relative safety from predators that is afforded sea birds in their oceanic habitats. In comparison, resources that can be used for breeding are much more restricted (Alerstam and Högstedt 1982). The competition for these limited resources has led to a variety of adaptations for breeding in the sea birds. The flight journey by the arctic tern from Antarctica to the desolate northern tundras and fiords is one of them.

ACKNOWLEDGMENTS

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THE INFLUENCE OF WEATHER ON ORIENTATION AND NUMBERS OF AVIAN MIGRANTS OVER EASTERN CANADA: A REVIEW

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ABSTRACT

This paper reviews the effects of weather on numbers of birds aloft, and on bird orientation and flight routes over southeastern Canada. New data concerning responses of different types of avian migrants to weather are given.

Each category of migrants tended to fly on occasions when winds were more or less following relative to its own direction of travel. However, many birds flew under calm conditions and some in cross or even opposing winds. Numbers aloft tended to be reduced under cloudy skies, but flight directions under overcast seemed little different from those under clear skies. There was no greater tendency for downwind flight under overcast than under clear skies.

Routes of migrants can be affected by proximate responses to weather, such as dawn reorientation when winds are unfavorable for continued flight in the original direction. Also, routes of some migrants are adapted to prevailing winds. For example, in autumn many birds fly over water, with following winds, from SE Canada to the West Indies. In spring they apparently return along a more westerly route where winds are more favorable.

INTRODUCTION

Weather can influence migrating birds in various ways. Average wind speeds are a substantial fraction of a bird's airspeed, such that a bird will make faster progress over the ground and use less energy to travel a given distance if it flies with following rather than opposing winds. A moderate crosswind will strongly influence track over the ground unless the bird makes a corresponding major adjustment in its heading through the air. In areas where there is a prevailing wind direction, wind patterns may influence migration routes; it will be easier to fly in some directions than in others. The occurrence of fog, cloud or precipitation has major implications for visual orientation mechanisms that use either celestial cues or landmarks.

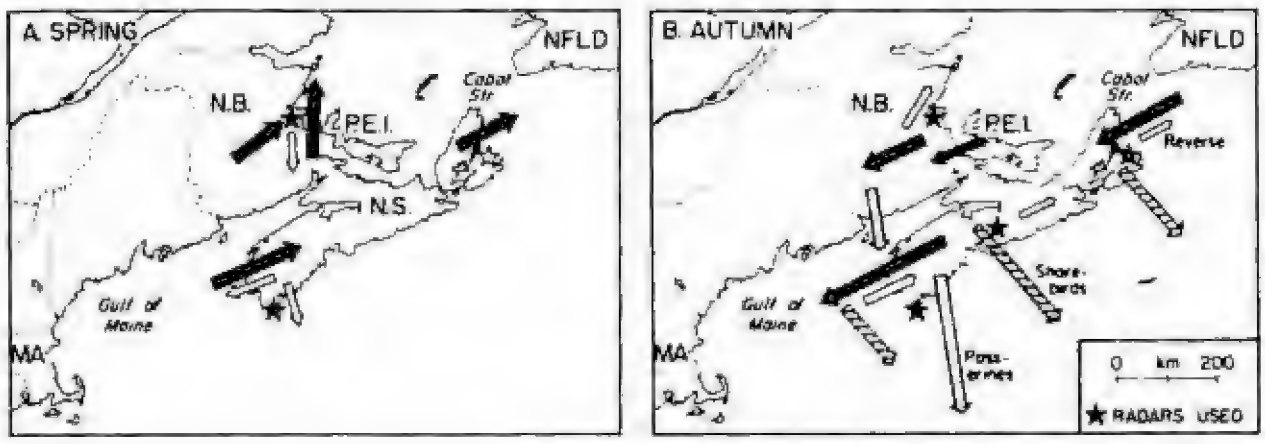

Figure 1
The main groups of migrants over SE Canada in (A) spring and (B) autumn.

This paper examines the effects of weather on numbers, orientation and routes of avian migrants by reviewing data from Nova Scotia and New Brunswick, Canada. I emphasize comparisons of the ways in which the various groups of migrants respond to weather. The detailed characteristics of migration in this area have been described elsewhere and are only summarized here.

Most spring data were obtained from two long-range surveillance radars, one in southwest Nova Scotia and one in New Brunswick (Fig 1A). In spring the predominant directions of migration are to the northeast, parallel to the coast, and to a lesser degree to the north (Richardson 1971). Reverse migration to the south and southwest involves far fewer birds, but occurs intermittently throughout the spring (Richardson, in preparation). During spring, birds are not seen arriving from the south, the direction of the West Indies.

Most autumn data were from three surveillance radars in Nova Scotia and one in New Brunswick (Fig 1B). More birds go SW, parallel to the coast, than in any other direction (Richardson 1972). However, small reverse movements to the NE occur intermittently throughout autumn (Richardson 1982a). In addition, there are SE flights of shorebirds and southward flights of passerines on certain dates; these birds are beginning nonstop flights to the West Indies or South America (Richardson 1979, 1980).

NUMBERS ALOFT VS. WEATHER

Numbers of migrants aloft over eastern Canada, as elsewhere, can differ by a factor of 100× or even 1000× from one day to the next and are strongly correlated with weather. A detailed review appears in Richardson (1978a); this section summarizes the main relationships in SE Canada.

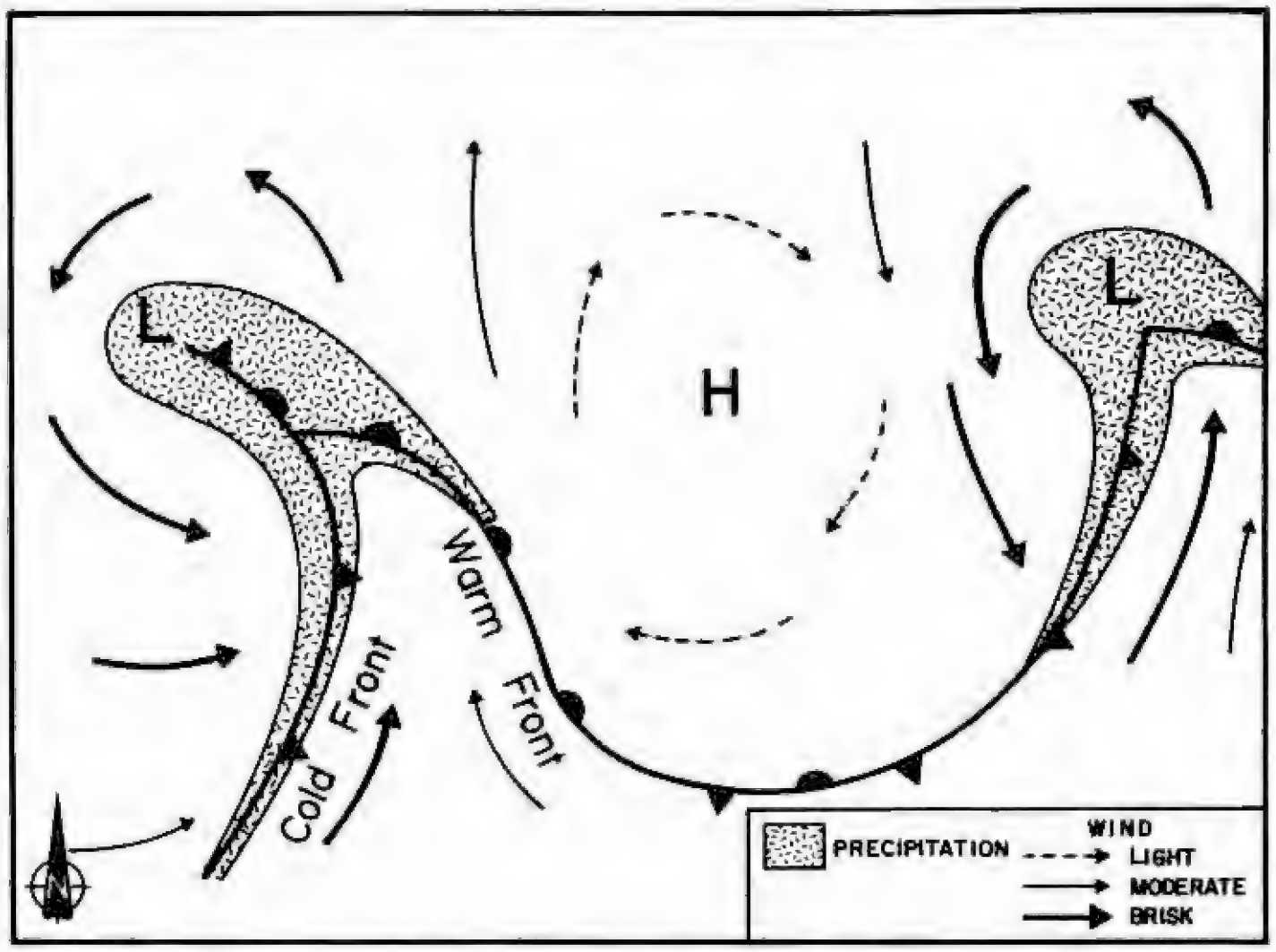

Figure 2
Typical configuration of high (H) and low (L) pressure systems, fronts, precipitation and winds at north temperate latitudes.

Pressure Systems, Fronts, and Wind

Weather patterns in eastern Canada are similar to those at any north temperate latitude (Fig 2). Low and high pressure areas move generally west to east. Winds are clockwise around highs and counterclockwise around lows. Thus winds are southerly when there is a high to the east, a low to the west, or both. Winds are northerly when there is a low to the east, a high to the west, or both. Winds are near calm near the center of a high. Precipitation and thick cloud are most likely when a low is near or when a front between air masses passes overhead.

Many studies in North America and Europe have shown that most bird species tend to migrate when winds are more or less following, relative to the preferred direction of those particular birds (Richardson 1978a). This is true in eastern Canada as well.

Far more birds fly N and NE over eastern Canada in spring on nights and days when there are following winds from the S or SW than on dates when winds are opposing. The association with following S and SW winds is even closer for the small number of birds that engage in NE reverse migration in autumn (Fig 3).

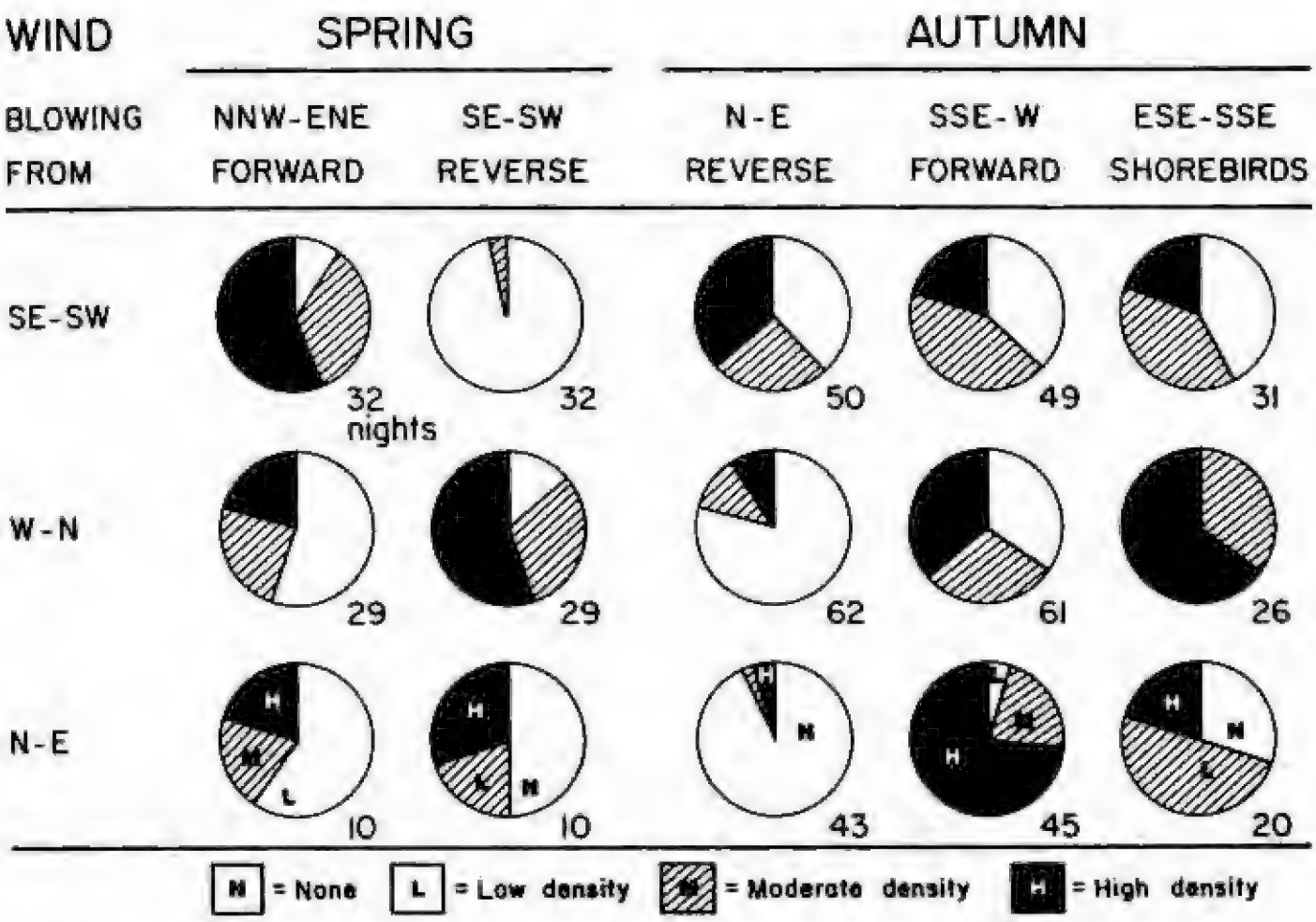

Figure 3

Amount of nocturnal migration of five types of birds detected over SE Canada with three categories of winds. Each circle shows the proportion of evenings when amount of migration was none or low, intermediate, and high.

In contrast, far more birds fly SW and S in autumn when there are following N and NE winds than with opposing southerly winds. Similarly, S and SW reverse migration in spring is strongly associated with following northerly winds.

In eastern Canada, as elsewhere (Richardson 1978a), groups of birds that travel in slightly different directions tend to fly with slightly differing weather. Shorebirds initiating SE flights toward the West Indies are significantly more likely to take off with NW following winds than with NE crosswinds (Fig 3; Richardson 1979). The predominantly SW flights of passerines, in contrast, tend to be denser on nights with NE following winds than with NW crosswinds (Fig 3). Furthermore, passerines that depart S toward the West Indies are more likely to fly with NW winds than are passerines that travel SW along the coast (Table 1). Thus, even excluding the extreme case of reverse migration, each group of migrants apparently prefers following winds relative to its own direction of travel.

Winds tend to be northwesterly soon after a cold front passes but often change to N or NE a day or so later as a high pressure area approaches. Thus, in both eastern Canada and elsewhere, SE migration often peaks immediately after a cold front passes, and SW migration peaks a day or so later (Richardson 1978a, p. 237).

Table 1
Occurrence of SW and SSE passerine migration over SW Nova Scotia in relation to broad-scale wind direction, autumn 1971.

Wind Direction	Number of nights when predominant migration direction was	
	SW	SSE
NW	7	8
NE	18	1

$\chi^2 = 9.95$, df = 1, $p < 0.005$

The association with following winds is by no means complete. Many birds fly under calm conditions, and some birds fly in cross and even opposing winds (Fig 3). Some categories and species of migrants show stronger preferences for following winds than do others (e.g., Alerstam 1978). Possible reasons for this variation in selectivity are discussed by Alerstam (1979a). Following winds will be especially important for birds that fly nonstop over inhospitable habitat, e.g., over the Atlantic Ocean from Nova Scotia to the West Indies in autumn. Without following winds, small landbirds probably could not complete this flight (Tucker 1975). Following winds may be less important for migrants flying short distances over habitat where they can land at any time.

Temperature and Pressure

Southerly winds tend to be accompanied by falling pressure and rising temperature as a high pressure area moves away to the east, a low approaches from the west, or both. It is not surprising that N and NE migrations, which are associated with southerly winds in both spring and autumn, tend to occur with falling pressure and rising temperature (Table 2). Conversely, northerly winds tend to be accompanied by rising pressure and falling temperature as a low moves away to the east, a high approaches from the west, or both. South and SW migrations also tend to occur with rising pressure and falling temperature.

Because of the close correlations among wind, temperature trend, and pressure trend, it is difficult to determine from uncontrolled field observations whether birds respond directly to pressure or temperature. Multivariate analyses sometimes indicate that numbers aloft are related to these variables even after the dominating correlations with wind have been taken into account (Richardson 1978a). This does not prove that birds respond to temperature and pressure, but it is suggestive. Direct responses to these variables might occur because they can be indicators of future food supply (e.g., insect availability), habitat suitability (e.g., freeze/thaw cycles), or winds aloft en route. Homing pigeons, at least, are remarkably sensitive to pressure change (Kreithen and Keeton 1974).

Table 2

Direction and significance of association between four weather variables and various categories of migrants over SE Canada during night (N) and day (D). Pluses (or minuses) indicate that the variable tended to assume higher (or lower) values when the specified type of migration was present[1].

Type of Migration and Main Flight Directions	24-hour Temperature Trend		6-hour Pressure Trend		Amount Opaque Cloud		Precipitation	
	N	D	N	D	N	D	N	D
Spring								
Forward (NNW–ENE)	+++	ns	– –	ns	– –	ns	– – – – – –	
Reverse (SE–SW)	– – – – – –		+++	+++	–	– – –	ns	–
Autumn								
Reverse (N–E)	+++	+++	– – – – – –		+	ns	**[2].	ns
Forward (SSE–W)	– – – – – –		+++	+++	– – – – – –		– –	ns
Shorebirds (ESE–SSE)	ns	ns	+	++	–	ns	– –	(*)[2]

[1] ns if $p > 0.1$, (±) if $0.1 \geq p > 0.05$, ± if $0.05 \geq p > 0.01$, ±± if $0.01 \geq p > 0.001$, and ±±± if $p \leq 0.001$. Based on Kruskal-Wallis tests of weather when amount of migration was zero vs. low vs. high, or below- vs. near- vs. above-normal.
[2] Nonlinear

Cloud and Precipitation

In general, fewer birds migrate when it is cloudy or raining than when it is clear (Richardson 1978a). However, this relationship is more precise for some categories of migrants than others. In some cases, especially for the variety of species migrating by day, no significant relationship was evident in SE Canada (Table 2).

Avoidance of flight with cloud or rain is probably advantageous for several reasons. Cloud may impair orientation by obscuring celestial or terrestrial cues. Also, cloud often occurs with low pressure areas, fronts, precipitation, and changeable winds. These conditions may require increased energy expenditure during or after flight, or may increase the probability of being blown off course or forced to the ground.

Able (1982) found that reverse migrations in the northeastern U.S.A. occur when prolonged overcast coincides with winds blowing toward seasonally inappropriate directions. In eastern Canada, NE reverse migration in autumn was the one type of movement positively associated with cloudy conditions (Table 2; Richardson 1982a). However, the correlation was weak, and cases of reverse migration occurred with every sky condition from overcast to completely clear.

Southward reverse migration in spring, like most other types of migration, was slightly *less* frequent under overcast than under clear skies (Table 2; Richardson, in preparation). Thus, impairment of visual orientation mechanisms by cloud cannot account for many of the cases of reverse migration in eastern Canada.

ORIENTATION VS. WEATHER

Flight Directions vs. Wind

Because most migrants in SE Canada tend to fly when winds are following relative to their usual flight directions, the overall distribution of tracks usually includes a large downwind component (Fig 4). This is so even when winds are blowing from the north in spring or the south in fall; reverse migration is a major component of total migration on those occasions. Some birds do move crosswind or even upwind, especially when winds are blowing in seasonally inappropriate directions. However, total numbers aloft in these latter situations are generally low (Fig 4).

The downwind tendency is not as strong in SE Canada (Fig 4) as in the SE U.S.A., where there is consistent downwind orientation by landbirds flying at night (Gauthreaux and Able 1970, Able 1974). In SE U.S.A. the few birds that take off when winds blow toward seemingly inappropriate directions orient downwind, as do the larger numbers flying with more favorable winds. In contrast, in SE Canada (Fig 4) and in the NE U.S.A. (Able 1982), some of the few birds taking off with seasonally inappropriate winds orient downwind, but many do not. Interpretation is hindered because there is little information about the species involved in the various types of flights detected by radar.

To further assess whether birds are actually orienting downwind using wind as a cue, I analyzed the tracks of various distinct categories of migrants over SE Canada (Richardson 1975, 1979, 1982a, in preparation). Daily mean tracks for each category of migration were significantly but usually weakly correlated with wind direction (e.g., Fig 5). Daily mean tracks usually were not precisely downwind, and tracks of individual birds were, of course, even more widely scattered. The slope of the regression of daily mean track vs. wind direction was always significantly less than 1.0 (Table 3). A slope of 1.0 would be expected if tracks were consistently downwind. Thus for each category of migrants, crosswinds seemed to deflect mean track from its average direction, but by only 36 to 66% of the deviation of the wind direction from following.

There are at least two possible explanations for such a pattern: uncorrected wind drift from fixed headings and "pseudodrift." The track over the ground is the vector sum of the bird's heading vector through the air plus the wind vector. Uncorrected drift occurs when birds fly on constant headings regardless of wind direction. Pseudodrift occurs when, even within a particular category of migrants, birds with slightly different preferred tracks fly selectively with winds that favor flight in their individual preferred directions.

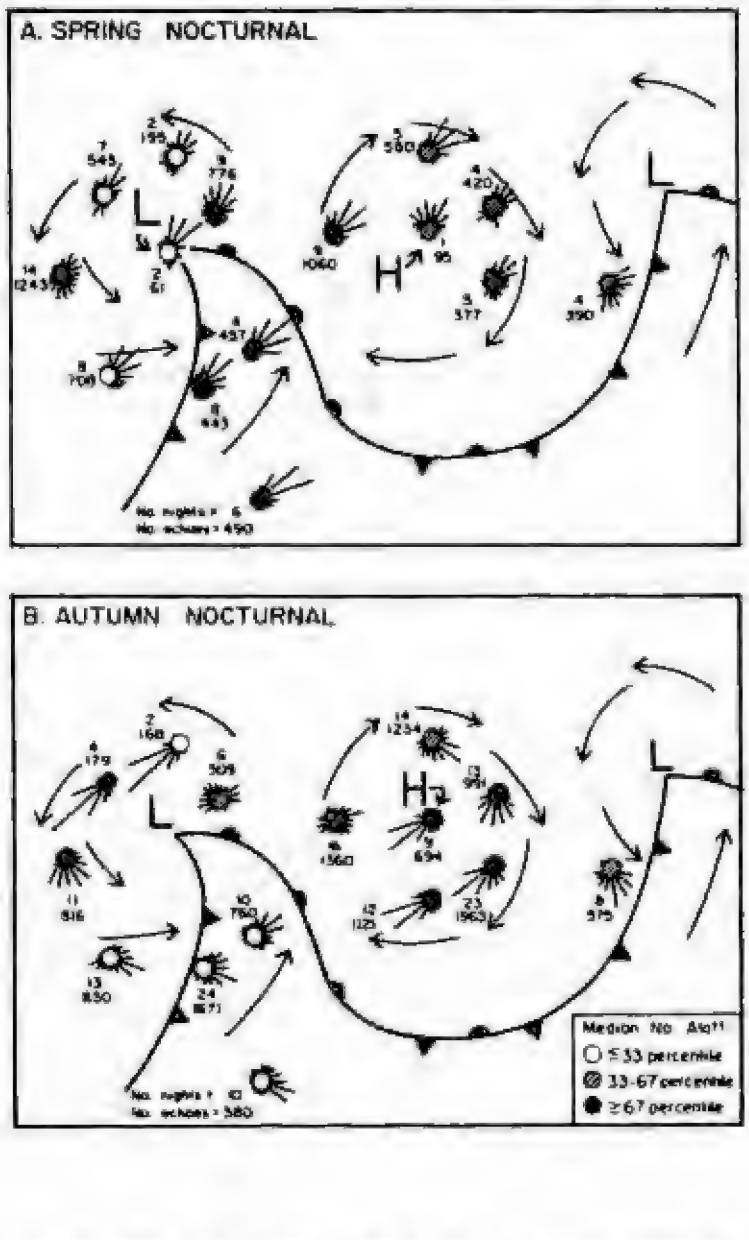

Figure 4

Directions of nocturnal migration over SE Canada with various types of synoptic weather. Each vector diagram is appropriately positioned with respect to pressure system and front locations and broad-scale wind patterns. Each vector diagram shows the percentage distribution of tracks of individual radar echoes. Total numbers aloft varied greatly among weather categories, as coded at the center of each vector diagram.

In the SE Canada study, there was insufficient information about winds aloft to distinguish between these two alternatives. In some studies, uncorrected wind drift has been found (e.g., Richardson 1976, 1982b) whereas in others the correlation between tracks and wind direction apparently represented pseudodrift (Alerstam 1976). Besides these two flight strategies and the "downwind flight" exhibited by many landbirds in the SE U.S.A., a fourth strategy has occasionally been found: maintenance of fixed tracks in a variety of winds through compensatory adjustments of heading (e.g., Drury and Nisbet 1964). Alerstam (1979a,b) has discussed the reasons why it may be advantageous for birds to drift in some situations and to correct for drift in others.

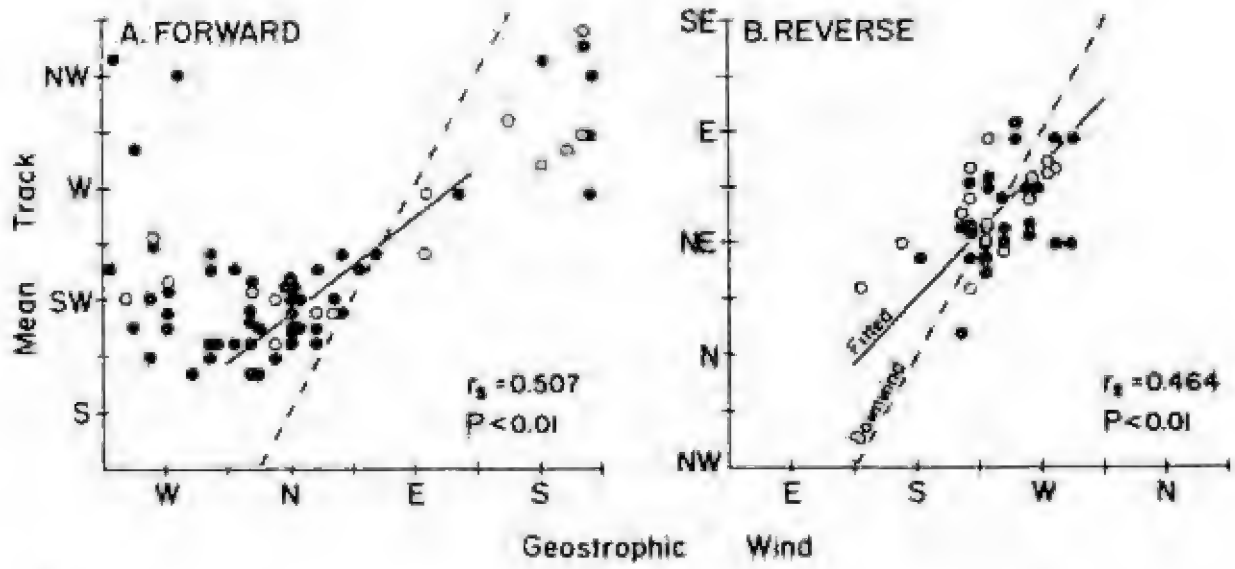

Figure 5

Mean tracks of migrants over Nova Scotia on autumn nights vs. geostrophic wind direction. Open symbols represent nights with 100% opaque cloud cover. Each symbol represents at least 10 radar echoes. Continuous lines were fitted by the geometric mean (GM) method (Ricker 1973). Only nights with winds in a 180° range were used in fitting the lines and in calculating Spearman rank correlations. The GM method is appropriate when the predictor variable is truncated (here to a 180° range) and subject to measurement error.

Orientation vs. Overcast

Birds flying over SE Canada on overcast occasions were not disoriented, and there was little evidence of deterioration in orientation. These results were similar to those of many earlier studies (Emlen 1975). Even under overcast, most birds moved along straight lines, at least within the limits of resolution of the radars used.

For most categories of migrants, variance among tracks was no greater under overcast than clear skies. The one category for which variance was greater with overcast was shorebirds departing SE on autumn nights ($p < 0.01$, Richardson 1979). Many of these shorebirds were probably above the clouds, and thus terrestrial rather than celestial cues may have been obscured. On the other hand, in spring the tracks of both forward and reverse migrants tended to be *less* variable on overcast than on clear occasions (Richardson 1975 and in preparation).

Perhaps we should not be surprised by reduced variance in tracks under overcast. Reduced variance might indicate deterioration, not improvement, in orientation. For example, birds with a variety of preferred directions and orientation mechanisms might switch to a single mechanism, e.g., downwind flight, when flying under overcast.

Nocturnal landbird migrants over the NE U.S.A. apparently tend to orient downwind when under overcast (Able 1982). If so in SE Canada, one would expect the deviation of track from downwind to be reduced on overcast occasions. However, multiple regression analyses for each category of migrants showed no strong tendency for this (Richardson 1975). Instead, mean tracks were correlated with wind direction in a similar manner under cloudy and clear skies (e.g., Fig 5). Furthermore, reverse migration (RM) over SE Canada cannot be fully explained as downwind flight with overcast and seasonally inappropriate winds (see above). RM in both spring and

Table 3

Regression of mean tracks of various categories of migrants over SE Canada on geostrophic wind direction[1].

Type of Migration and Main Flight Directions	Wind Direction (from) Considered	Night			Day		
		Slope[1]	r_s[2]	*n*	Slope	r_s	*n*
Spring							
All Forward (NNW–ENE)	ESE–SSW–WNW	0.51	0.61	46	0.50	0.63	37
Passerines (NNE–ENE)	SE–SW–NW	0.36	0.45	27	–	–	–
Reverse (SE–SW)	W–N–E	0.66	0.51	29	0.57	0.61	31
Autumn							
Reverse (N–E)	SE–SW–NW	0.60	0.46	42	0.51	0.25	70
Forward (SSW–WNW)	NW–NE–SE	0.43	0.51	36	0.38	0.35	41
Shorebirds (ESE–SSE)	SW–NW–NE	0.44	0.42	47	0.40	0.57	43

[1] The geometric mean method (see Fig 5) was applied to occasions when winds were following or side. All slopes are significantly more than 0.0 but significantly less than 1.0 ($\alpha = 0.05$).

[2] Spearman rank correlation.

autumn occurred on both clear and overcast occasions.

Overcast had a more conspicuous effect on numbers aloft than on orientation. The reduced tendency to fly under overcast may be partly a result of the reduced range of orientation mechanisms usable when celestial or terrestrial cues are obscured. However, orientational problems are probably only one of several factors causing selection against individual birds that fly on cloudy occasions (see above).

ROUTES VS. WEATHER

Results from SE Canada illustrate (1) adjustments in routes of individual migrants in response to current weather, and (2) adaptation of large-scale migration patterns to prevailing wind patterns.

Dawn Reorientation of Landbirds

Landbirds that take off from Newfoundland and eastern Nova Scotia in the evening and fly SW may be over water east or south of Nova Scotia at dawn (Fig 1B). Around dawn, these birds sometimes turn to the NW, the direction likely to return them to land most quickly (Baird and Nisbet 1960, Murray 1976). However, on other mornings they continue SW (Richardson 1978b). Birds continuing SW, generally parallel to the coast, will not reach land for at least several hundred kilometers (no closer than Cape Cod, MA; possibly not until Cape Hatteras, NC).

On mornings when landbirds continue SW over the ocean, the wind is from the north or NE—favorable for continued SW flight and less favorable for NW flight back to land (Richardson 1978b). On mornings with other winds, especially opposing SW or W winds, the birds reorient from SW to NW and attempt to return to land. A bird's route will be quite different depending whether it continues SW or reorients NW at dawn. The route followed by these migrants seems largely determined by the winds encountered over the sea around dawn.

Migration from SE Canada to the West Indies

Some shorebirds and landbirds fly SE or S from Nova Scotia and New England toward the West Indies in autumn, but there is little or no reciprocal flight in spring. This is apparently an adaptation to prevailing wind patterns (Richardson 1974, 1976; Gauthreaux 1980). Weather over the western Atlantic is dominated by the so-called Bermuda high, which results in prevailing northerly winds east of Bermuda and southerly winds closer to the coast (Fig 6). Near the West Indies, the wind is almost always easterly.

Birds leave the coast in NW winds behind cold fronts (see above). Post-frontal following winds usually persist along the first 1/4−1/3 of the overwater route to the West Indies. Thereafter the birds are in the zone of prevailing following winds east of the Bermuda high, or in the light winds near the center of the high (Fig 6). South of Bermuda, mean tracks shift to S or SSW, and the birds usually arrive at the West Indies with side or partly following easterly winds (Richardson 1976, Williams and Williams 1978). Thus these birds usually encounter following or partly following winds throughout the nonstop flight to the West Indies. Flight altitudes range from low to extremely high (>6 km). Some birds may select altitudes with optimum winds (Richardson 1976, Alerstam 1981), although evidence on this point is inconclusive (Williams 1985).

Birds that fly SW down the coast to Florida and then SE along the West Indies avoid the long overwater flight but must travel much farther, largely against the prevailing winds (Fig 6). Many landbirds do fly SE along the West Indies (Richardson 1976). However, the disadvantages of this route apparently are sufficient to make it adaptively advantageous for many birds to fly along the "downwind" overwater route from SE Canada to the West Indies.

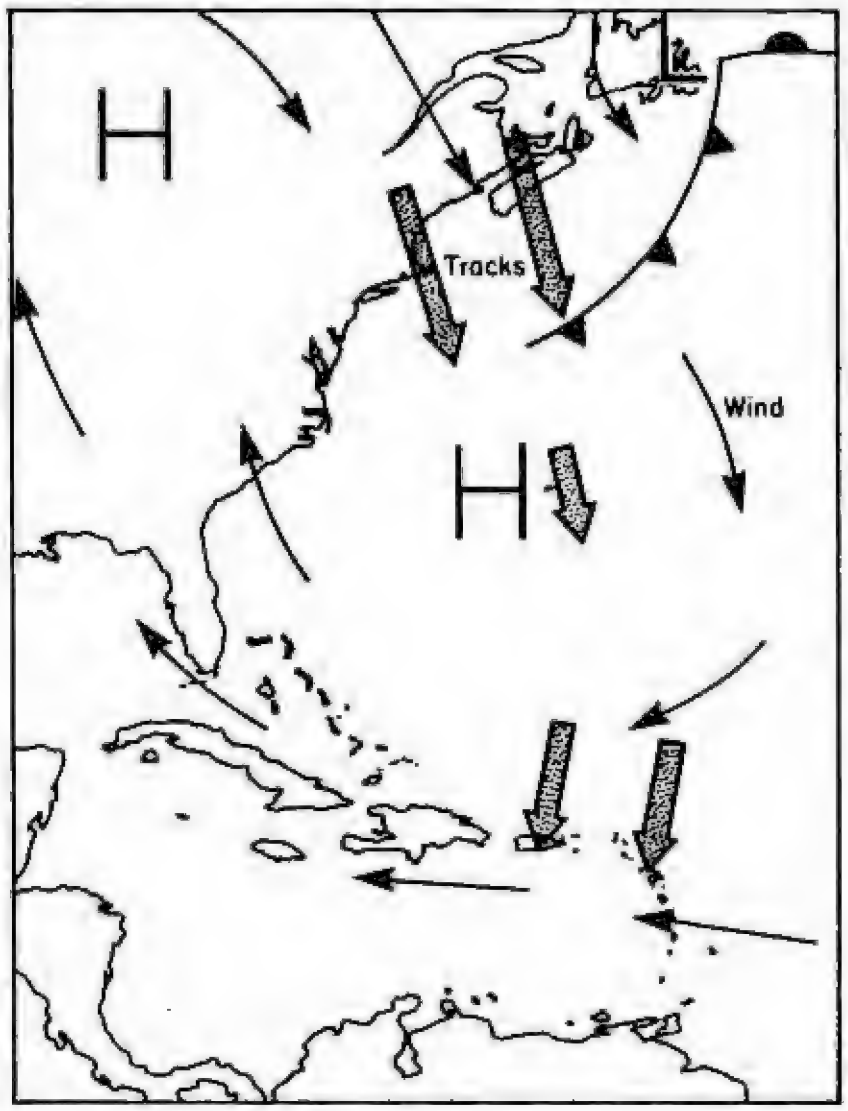

Figure 6
Typical weather over the western Atlantic when birds depart from SE Canada toward the West Indies in autumn.

Winds over the western Atlantic in spring are similar to those in autumn. These winds are favorable for NW flights from the West Indies toward Florida, and then for N and NE flights over the mainland and coast (Fig 6; Gauthreaux 1980). In contrast, winds do not favor northward flight over the ocean directly to eastern Canada. Radar observations in Puerto Rico show that spring migrants do indeed depart mainly to the NW; very few depart to the north (Richardson 1974).

This paper summarizes some but not all ways in which weather can affect the timing, orientation and routes of migration. Other influences not discussed here include the effects of weather in concentrating or dispersing birds at leading lines, the importance of updrafts to soaring birds, and weather-induced mortality during migration. I have also mentioned only a few of the important theoretical analyses and experimental studies that have been done. However, the data from eastern Canada do demonstrate that weather can influence avian migrants profoundly.

ACKNOWLEDGMENTS

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CHAPTER SIX

INSECT MIGRATION

Insects offer at least two major advantages as subjects for studies of the mechanisms and adaptive significance of migration. The first of these is their small size and the consequent relative ease with which large numbers can be reared in the laboratory. Laboratory analysis of behavior and physiology can thus be iterated with field studies of movement, seasonal cycles, and the population dynamics to integrate the details of energetic or life table processes with those of natural history and ecology. Such integration goes far toward closing the gaps between proximate and ultimate explanations of migration as the papers which follow amply demonstrate. The large sample sizes possible with insects help to overcome the problems inherent in the variance of migratory behavior occurring in both laboratory and field.

The second advantage to insects is their diversity, both of taxa and modes of migration. Insects are apparently the most speciose organisms on earth and along with this taxonomic diversity is a diversity in the ways they migrate. Some of this variation is in the scale of migration. We are by now familiar with the spectacular movements of certain locusts, lepidopterans and other relatively large insects which can be continental or even intercontinental in scope. But even more common are the equally significant (for life histories) migrations of numerous small species such as aphids, whose movements may cover only hundreds or even tens of meters. Any sampling of the aerial "plankton" reveals a veritable rain of species moving from one locale to another (Johnson 1969). We know the details for very few of these species. Also astonishingly diverse are the patterns and pathways of migration. Most insects fly, but some balloon on silk, some use phoresy, some march in swarms, and there is even an aphid whose first instars walk on water (Foster and Treherne 1978). Alternatives for flying insects include continuous variation in programmed flight duration, degrees of histolysis of the flight muscles, and life cycle partitioning by dimorphism or polymorphism of wing structure from macrotpery to aptery (Dingle 1980). Understanding of the array of mechanisms and of the adaptive significance of these diverse developmental physiologies and life styles affords a considerable challenge to migration biologists.

The gain in understanding of migration mechanisms promoted by studying insects under controlled laboratory conditions is clear from five of the studies included in this section. M. A. Rankin reviews many aspects of flight behavior and metabolism that have been analyzed in the laboratory and shows that in very diverse taxa juvenile hormone controls both flight and reproduction. She demonstrates clearly

the evolution of suites of covarying traits linked by physiology. W. S. Herman examines the hormones of the monarch butterfly in detail, outlining the role of juvenile hormone and two additional hormones, apparently peptides, in various aspects of the life cycle from mobilizing energy reserves to maturation, reproduction and flight. J. O. Palmer shows nicely how insects can be used for quantitative genetic studies of migration and demonstrates via selection on wing length and correlated responses in flight and fecundity that migration is part of a life history syndrome with an architecture of genetic correlations. His unambiguous results derive from the large samples in his selected lines. A. J. Zera examines the genetics of wing polymorphism in gerrids and demonstrated clear genotype by environment interactions in a complex polygenic system. The higher winter survival but lower fecundity of winged morphs relative to apterous forms indicates the potential for energetic constraints and trade-offs in wing polymorphic systems. Finally, M. L. McAnelly iterates laboratory and field studies to show that differences in migratory behavior observed in field populations of the grasshoppers ***Melanoplus sanguinipes*** from various locations remain when the animals are reared and tested under similar conditions in the laboratory. The differences thus appear to be genetic and to have been selected for rather than to be responses induced by proximate local environmental effects

As McAnelly's study illustrates, field studies are necessary if we are to sort out the adaptive significance of insects of migration. This is further shown in the papers which deal primarily with studies undertaken under natural conditions. L. P. Brower summarizes the many years of field research on the spectacular migrations and overwintering aggregations of the monarch butterfly leading to our current understanding of the long distance round-trip movements of this species. At the same time he points out the many important questions still unanswered. L. E. Gilbert and T. J. Walker also deal with butterfly migrations. Gilbert analyzes the relation between rainfall, host plant phenology, and outbreak and migration patterns of two species in the shrublands of southern Texas, while Walker uses directional trapping techniques to discern boundary layer migration and orientation patterns in four species migration through northern Florida in the Autumn. Orientation parallel to the axis of the Florida Peninsula is remarkably precise, but the mechanisms are unknown. R. F. Denno takes a detailed look at the adaptive significance of wing polymorphism in salt marsh homopterans and shows the relations among seasonal changes, host plant nutrition, and crowding in influencing the frequency of the wing morphs and the influence of migration on population dynamics. C. Solbreck surveys data on forest and milkweed insects in northern Europe to show how individuals may benefit from migration and how populations can be affected.

Any symposium such as this is necessarily eclectic in its choice of subject matter, and this one is no exception. We have, for example, barely touched on the insect species available for studies of insect migration. It is also obvious that certain relatively well-studied insects, such as aphids and locusts, are absent from our survey. The studies reported here do, however, give a good notion of the breadth and depth of our knowledge. Some trends are apparent such as the primary role of juvenile hormone in orchestrating life cycles and migration in allowing adjustment of life

histories to seasonal, and in some cases more unpredictable, changes is also evident. But as all the participants show, there is still much that is not known and therefore much to be done and much to be learned of both the how and why of migration.

Hugh Dingle

FITNESS, POPULATION DYNAMICS AND MIGRATION IN PLANTHOPPERS: THE ROLE OF HOST PLANTS

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ABSTRACT

Planthopper (Homoptera: Delphacidae) populations are composed of two wing forms, flightless brachypters and macropters that can fly. There are no consistent differences in development time of the nymphs or fecundity between wing-forms. However, brachypters have a shorter preoviposition period than macropters resulting in earlier age to first reproduction. Nymphs which feed on more nutritious hosts eclose as larger adults. Fecundity and body size appear to be positively related. Crowding extends development time and results in smaller adults. The negative effects of crowding are in part ameliorated if planthoppers feed on nutritious hosts. On marginal host plants there is a density-dependent migration response that is moderated on more nutritious hosts. In laboratory choice tests, macropters prefer to feed and oviposit on nutritious, compared to nutrient-deficient, host plants. On a large scale in the field, macropters can discriminate and colonize superior quality hosts. Therefore larger, more fit offspring are produced. Brachypters are relatively immobile and lack this ability. For ***Prokelisia marginata***, 81% of adults are macropters. This wing-form pattern is unique compared to other salt marsh-inhabiting planthopper species and is related to the patch dynamics of its host plant which provide the opportunity for interhabitat migration.

INTRODUCTION

Emphasis in the life history literature has focused on reproductive traits such as fecundity and age to first and peak reproduction (e.g., Stearns 1976, 1977). Equally important to an organism is the ability to place offspring on appropriate resources, and failure to do so can have drastic effects on fitness (van Emden 1966; McClure 1980; Whitham 1978, 1979, 1980). Consequently, behaviors like migration and diapause that synchronize reproduction with favorable resources in space and time must be viewed as integral features of insect life history (Southwood 1962, 1977; Dingle 1972, 1974, 1979, 1982; Denno and Dingle 1981; Denno 1983).

Southwood (1977) and Solbreck (1978) have provided theoretical perspective on the evolution of migration and diapause. In the course of evolution, members of a species will evolve those life history traits which maximize the number of their descendants in the habitat, where habitat is viewed in the two dimensions of "time" and "space" (Southwood 1977). Organisms must choose between reproducing "now" and "later" in time and between "here" and "elsewhere" in space. The evolutionary choices herbivores make depend on dynamical changes in the suitability of the host plants they exploit. For herbivorous insects like planthoppers and aphids, host plant nutrition, the density of predators, parasites, pathogens, competitors, and physical factors all influence the suitability of the host plant patch. If changes in host plant suitability resemble each other in patches here and elsewhere, then diapause rather than migration should be favored when all patches simultaneously deteriorate (Fig 1A). On the other hand, if changes in host plant suitability among patches are out of phase, migration should be favored because as conditions deteriorate here, they are improving elsewhere (Fig 1B). Solbreck (1978) has also suggested that migration will be favored where an herbivore inhabits a relatively persistent habitat here year-round, but has the seasonal opportunity to exploit temporary hosts elsewhere (Fig 1C).

Large herbivores like browsing mammals, birds and even some butterflies are able to effectively exploit the current patch and then move on as individuals if conditions take a turn for the worse. However, the contingencies associated with tracking variable resources can be very different, particularly to small animals like insects, and the tracking cannot always be accomplished by a singe phenotype (Levins 1968; Denno 1979, 1983; Harrison 1980). The very characteristics that allow for the successful colonization of alternative patches elsewhere (e.g., low wing-loading and reduced or delayed reproduction) may prevent an individual from effectively exploiting the current patch. Consequently, selection may favor a polymorphism where each morph is successful under a different set of conditions. Examples are the long-winged (macropters) migrants and flightless forms (short-winged brachypters and apters) of planthoppers and aphids (Lees 1966, 1967; Denno 1976, 1978, 1979, 1983), the migratory and solitary phases of locusts (Kennedy 1956, Dempster 1963) and the migratory and nonmigratory forms of milkweed bugs (Dingle 1978, 1981). Ultimately, the wing-form or flight-form composition of a population will depend on the relative favorableness, permanence, predictability and isolation of the resource patches it exploits (Southwood 1962, 1977; Southwood, May, Hassell and Conway 1974; Denno 1978, 1979, 1983; Solbreck 1978; Denno and Grissell 1979; Denno, Raupp, Tallamy and Reichelderfer 1980).

In this report I focus on a single species of wing-dimorphic planthopper, ***Prokelisia marginata*** (Van Duzee) to show the mediating role host plants play in the population dynamics of herbivores and in the evolution of their life histories. ***P. marginata*** is a sap-feeding homopteran that feeds mostly on the contents of phloem cells of the perennial intertidal grass ***Spartina alterniflora*** its only host in eastern North America. *S. **alterniflora*** dominates the vegetation of Atlantic and Gulf coast marshes where it grows primarily below mean high water level in large pure stands. ***Prokelisia marginata*** is by far the most abundant herbivore on ***Spartina alterniflora***

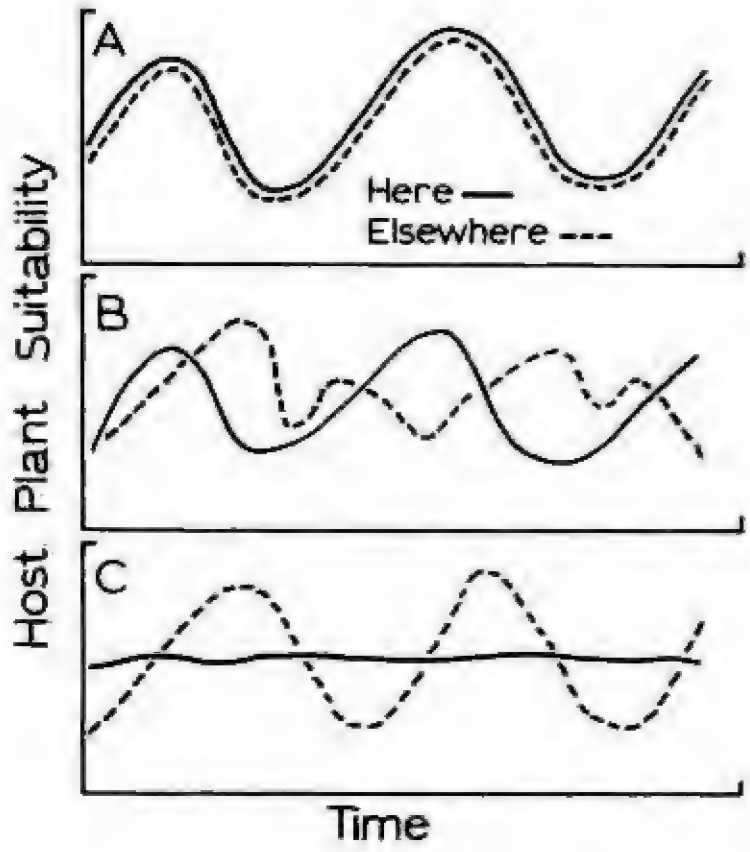

Figure 1

Predicted life history responses of herbivorous insects to spatial and temporal changes in the suitability of host plants in patches "here" (solid line) and "elsewhere" (broken line). (A) Where changes in the suitability of hosts in patches here and elsewhere are similar, better alternatives are not available, and diapause rather than migration is favored when the quality of hosts is low in all patches. (B) If the suitability of hosts improves elsewhere while those in the current patch deteriorate, then migration should be favored. (C) If suitable host plants are permanently available in one habitat here yet fluctuate seasonally elsewhere, migrations to and from the temporary habitat can occur. Modified from Solbreck (1978).

(Denno 1983). With saw-like ovipositors, females insert their eggs between the ridges on the upper blade-surfaces of the grass. Eggs hatch and nymphs feed on site, passing through 5 instars. In the mid-Atlantic states there are 3 generations per year, and nymphs overwinter by nestling into the thatch of the grass (Denno 1983).

My specific objectives for this chapter are these: First, I compare the ecological and behavioral characteristics of the wing-forms of planthoppers in light of their performance on changing host plants. Second, I consider factors that contribute to the deterioration of the current patch of hosts and how these interact to reduce planthopper fitness. Third, cues that signal patch deterioration and trigger migration and escape are addressed. Fourth, I consider the ability of migrants to discriminate and select superior host plants from a mosaic of less favorable ones. Last, I relate interhabitat migration and the unique life history of ***Prokelisia marginata*** to dynamical features of its host plant.

DEVELOPMENTAL, REPRODUCTIVE AND BEHAVIORAL CHARACTERISTICS OF PLANTHOPPER WING-FORMS

Populations of planthoppers are usually composed of two discrete wing-forms (Kisimoto 1965; Mochida 1970; Drosopoulos 1977; Denno 1978, 1979, 1983). There are long-winged macropters that can fly and short-winged brachypters that cannot. Macropters are capable of long distance flight and consequently are able to escape from unfavorable host plants and colonize new ones (Denno and Grissell 1979, Denno et al. 1980). Because of their flightlessness, brachypters can move only short distances up to several meters and are unable to track large-scale changes in the abundance and quality of their host plants (Raatikainen 1967, Denno et al. 1980, Denno 1983).

Because macropters must build wings and flight muscles, as well as allocate energy to the biochemistry of flight, one might expect differences in development or fecundity compared to brachypters that are not saddled by the constraints of flight. For aphids this is certainly true; winged alates are significantly less fecund than the flightless apterae (Dixon and Wratten 1971; Dixon 1972; Taylor 1975; Wratten 1977; Dixon and Dharma 1980; but see Dingle, this volume). However, in planthoppers the pattern is not quite so clear. I have compared the nymphal development time, preoviposition period and fecundity between the brachypters and macropters of several species of planthoppers including ***Prokelisia marginata*** in Table 1. There is no significant difference between the nymphal development time of the macropter and brachypter for either ***Prokelisia marginata*** or ***Javesella pellucida***. Furthermore, a sign test performed on the development times of the macropters and brachypters for all species included in the Table found no significant difference (p = 1.000 ns). Also, where tested by the various authors, there was no significant difference between the fecundity of either wing-form. A sign test also bears out this result for all species in Table 1 (p = 0.180 ns). Despite the similarity in fecundity and nymphal development time, there is a consistent difference in the length of the preoviposition period between the wing-forms of planthoppers. Brachypters have a shorter preoviposition period than macropters (sign test, p = 0.002) and consequently an earlier age to first reproduction.

Perhaps the most striking difference between the wing-forms of planthoppers is a behavioral one. Laboratory observations show that the macropters of ***Prokelisia marginata*** are very "nervous" and upon disturbance quickly release from their holds. Brachypters, on the other hand, are more reluctant to jump from their host plant and are much less responsive (Denno 1983). Together, immobility and early age to first reproduction may function to allow brachypters to remain on their immediate host plants and exploit them more effectively than their long-winged counterparts. The fact that outbreaks of planthoppers and heavy host plant damage are often associated with the occurrence of brachypters (Kisimoto 1965, 1977; Mochida and Dyck 1977) is consistent with this hypothesis. Thus as long as host plants remain favorable in the current patch, the brachypter should be the optimal wing-form, particularly if the patch occurs in a climatically harsh habitat where it is adaptive to offset high mortality with an earlier age to first reproduction.

Table 1

Comparison of the nymphal development time (days), preoviposition period (days), and total fecundity of brachypterous (B) and macropterous (M) female planthoppers.

Species	Nymphal Development		Preoviposition Period		Fecundity		Reference
	B	M	B	M	B	M	
Mullerianella fairmairei			5.6	9.4[a]	357	331 ns	Drosopoulos (1977)
Mullerianella brevipennis			7.0	10.0[a]	161	155 ns	Drosopoulos (1977)
Nilaparvata lugens	14.7	15.4	2.7	6.0	599	543	Kisimoto (1965)
Niliparvata lugens	18.0	20.3					Kisimoto (1965)
Nilaparvata lugens							Mochida (1970)
genotype +/+	14.3	14.1	1.5	6.2	300	249	
genotype +/r	14.7	14.5	2.7	6.8	126	174	
genotype r/r	14.2	14.0	2.9	7.2	43	106	
Niliparvata lugens							Oh (1979)
1st mating					289	294 ns	
2nd mating					141	135 ns	
3rd mating					74	52	
Javesella pellucida	29.2	32.2 ns	5.4	7.1[a]	156	156 ns	Mochida (1973)
Sogata furcifera			2.9	3.7	484	385	Kisimoto (1965)
Sogata furcifera	12.9	14.3					Kisimoto (1956)
Laodelphax striatella	14.9	16.6					Kisimoto (1956)
Laodelphax striatella			3.0	5.0	555	570	Kisimoto (1965)
Laodelphax striatella					158	119	Tsai et al. (1964)
Laodelphax striatella					106	61	Nasu (1969)
Prokelisia marginata	37.9	37.4 ns	7.3	8.5	81	77 ns	Denno (this report)
Consensus[b]	B = M		B < M		B = M		

a = $p < 0.01$

ns = not significant

b = Consensus decisions determined by sign test (Siegel 1956).

PATCH DETERIORATION: EFFECTS OF HOST PLANT NUTRITION AND CROWDING ON PLANTHOPPER FITNESS

The fitness of many species of planthoppers and aphids is improved when they feed on nutritionally superior host plants. For example, when they are fed plants containing a higher concentration of soluble or amino nitrogen, planthoppers and aphids obtain a larger body size, realize greater fecundity and achieve larger populations than they do when fed less nutritious hosts (Table 2). When nymphs of *P. marginata* develop on fertilized seedlings of *Spartina alterniflora*

Table 2
Responses of Homoptera to increased plant nitrogen

Taxon	Body Size	Fecundity	Population	Reference
Aphididae				
Drepanosiphum platanoides	+ (amino N)	+ (amino N)	+ (amino N)	Dixon (1970)
Acyrthosiphon pisum		+ (amino N)[a]		Auclair (1976)
Brevicoryne brassicae		+ (soluble N)[a]		van Emden (1966)
Myzus persicae			+ (nitrogen)[a]	van Emden (1966)
Myzus persicae			+ (nitrogen)[a]	Vijverberg (1965)
Tuberolachnus salignus			+ (nitrogen)[a]	Vijverberg (1965)
Delphacidae				
Nilaparvata lugens		+ (amino)[a]		Sogawa (1977)
Niliparvata lugens			+ (nitrogen)[a]	Mochida et al. (1977)
Saccharosydne saccharivora			+ (nitrogen)[a]	Mochida et al. (1977)
Perkinsiella vitiensis			+ (nitrogen)[a]	Mochida et al. (1977)
Prokelisia marginata	+ (nitrogen)[a]	+ (nitrogen)[a]	+ (nitrogen)[a]	Vince et al. (1981)
Prokelisia marginata	+ (soluble N)[a]		+ (soluble N)[a]	Denno (1983, this report)

+ = positive response
a = plant nitrogen increased by fertilization

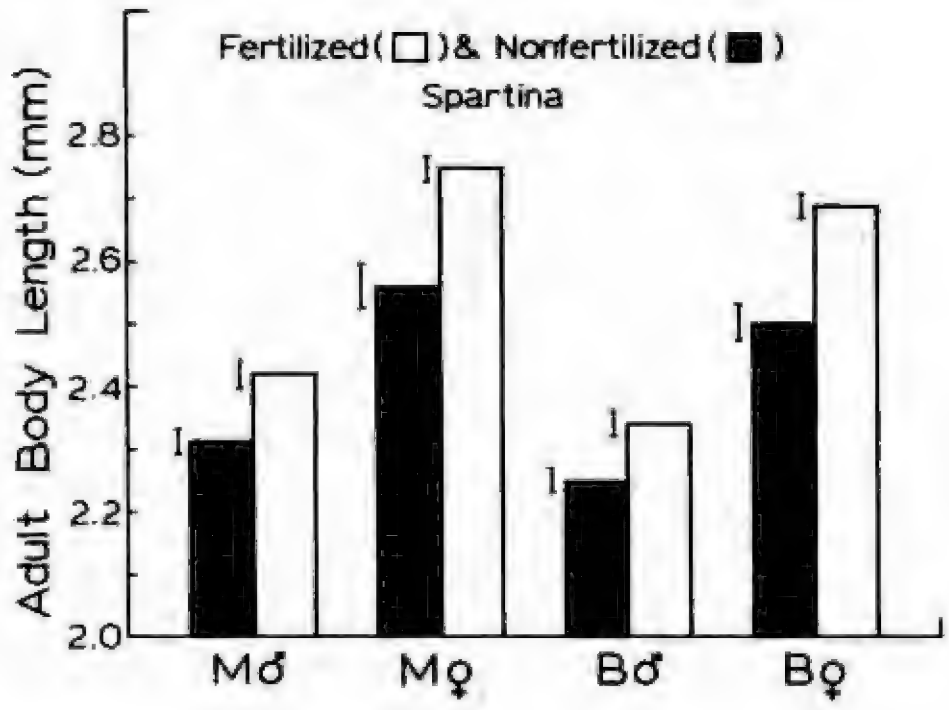

Figure 2
Body lengths of the sexes and wing-forms of *Prokelisia marginata* raised on heavily fertilized ($\bar{x}$ = 61.5 ± 7.4 mg·g^{-1} soluble protein) and lightly fertilized ($\bar{x}$ = 15.5 ± 4.3 mg·g^{-1} soluble protein) seedlings of *Spartina alterniflora*. All sexes and wing-forms were significantly larger when raised on fertilized seedlings ($p < 0.05$). M = macropter, B = brachypter. Standard errors surround means.

($\bar{x}$ = 61.5 ± 7.4 mg·g^{-1} soluble protein), they eclose as significantly larger adults compared to nymphs fed nutritionally inferior seedlings ($\bar{x}$ = 15.5 ± 4.3 mg·g^{-1}

Table 3
Life history correlates in the Homoptera

Taxon	Body Size-Fecundity	Body Size-Longevity	Longevity-Fecundity	Reference
Aphididae				
Drepanosiphum platanoides	+	+		Dixon (1970)
Aphis fabae	+	0		Dixon and Dharma (1980)
" "	+			Dixon and Wratten (1971)
" "	+	+	+[a]	Taylor (1975)
Acyrthosiphon pisum	+			Murdie (1969)
Pemphigus betae	+			Whitham (1978,1981)
Membracidae				
Umbonia crassicornis	+			Wood and Dowell (1984)
Delphacidae				
Nilaparvata lugens			+	Mochida (1970)
Javesella pellucida				Mochida (1973)
Prokelisia marginata	+			Denno (this report)

+ = positive relationship, 0 = no relationship

a = There is a size-dependent survival threshold below which fecundity depended upon longevity and above which longevity and fecundity were independent.

Table 4
Effect of crowding on Homoptera fitness.

Taxon	Development Rate	Mortality	Body Size	Fecundity	Reference
Aphididae					
Drepanosiphum platanoides		+	−	−	Dixon (1970)
Aphis fabae			−		Way and Banks (1967)
" "			−	−	Way (1968)
Acyrthosiphon pisum			−	−	Murdie (1969)
Delphacidae					
Nilaparvata lugens	+	+			Kisimoto (1965)
Mullerianella fairmairei	+				Drosopoulos (1977)
Javesella pellucida	0	+			Mochida (1973)
Prokelisia marginata	+		−	−	Denno (this report)

+ = positive relationship with crowding, 0 = no relationdship with crowding,
− = negative relationship with crowding.

soluble protein; Fig 2). Furthermore, there is a significant positive relationship ($r = 0.689$, $n = 11$, $p < 0.01$) between total female fecundity and body size for *P. marginata*. Using this relationship to predict fecundity, the females fed nutritionally superior *S. alterniflora* seedlings as nymphs (Fig 2) should realize a 20−25% increase

in total fecundity (also see Denno and McCloud, in press). Generally, there are positive relationships between body size, fecundity and longevity throughout the Homoptera (Table 3). Apparently, for animals like planthoppers and aphids, fecundity and longevity are mediated in part by body size.

Crowding generally reduces fitness in planthoppers and aphids (Table 4). At high densities nymphs develop slower, incur greater mortality and eclose as small adults with reduced fecundity. However, there is an interesting interaction between crowding and host plant nutrition (Denno, Douglass and Jacobs, in press A). When nymphs of ***P. marginata*** are reared under equally crowded conditions on both heavily fertilized and lightly fertilized seedlings of *Spartina*, the adults which eclose on the nutritionally superior plants are significantly larger. Apparently, the negative effects of crowding on body size, seen when animals are raised on marginal hosts, are in part ameliorated if nymphs feed on high quality *Spartina*.

As the season progresses on the high marsh, there is a decline in the nutritional quality of *Spartina* (Denno 1983). Together with high levels of crowding incurred by nymphs of ***P. marginata*** during summer, decreases in plant nitrogen contribute to reduction in planthopper fitness. Furthermore, planthoppers themselves may contribute to the demise of the local patch. Heavy feeding and oviposition by the brown planthopper ***Nilaparvata lugens*** on rice results in chlorosis and even plant death (Mochida, Suryana and Wahyu 1977). Similar kinds of damage can be seen on *Spartina* as a result of feeding and oviposition by ***P. marginata*** (Denno 1983). In fact, for other sap-feeding insects, Franz (1958) and McClure (1977) have shown how previous feeding by woolly aphids and scale insects reduces host plant quality, making hosts less suitable for subsequent attack. In the section that follows I discuss what environmental cues are used by planthoppers to signal the deterioration of the local patch and trigger the migration response.

PATCH DETERIORATION, WING-FORM DETERMINATION AND THE MIGRATION RESPONSE IN PLANTHOPPERS

Based on reciprocal crosses between brachypters and macropters of several pest species of planthoppers, Kisimoto (1956, 1965) and Raatikainen (1967) concluded that wing-form is not inherited by any simple genetic rule. Wing-form is mediated by an individual's response during the nymphal stage to a suite of environmental cues that signal the deterioration of the local patch. As long as conditions remain favorable on the current resource, a developmental switch responds with the production of a short-winged adult. However, if conditions become less favorable, a long-winged adult may result (Denno and Grissel 1979, Denno et al. 1980).

Poor plant nutrition and crowded conditions incurred during the nymphal stage lead to the production of macropters in several species of planthoppers (Kisimoto 1956, Johno 1963, Raatikainen 1967, Mochida and Kisimoto 1971, Mochida 1973, Drosopoulos 1977). Johno (1963), Mochida and Kisimoto (1971) and Mochida (1973) have shown that high densities of nymphs lower the nutritional quality of host plants, which indirectly results in the production of macropters. Photoperiod may have major

effects on the determination of wing-form in some species (Drosopoulos 1977), yet not in others (Kisimoto 1956). For ***Prokelisia marginata*** Denno (1983) reasons that photoperiod very likely plays little role in wing-form determination.

Denno (1976, 1983), Denno et al. (1980), and Strong and Stiling (1983) have implicated crowding as a proximate determinant of wing-form in ***Prokelisia marginata***. To test more rigorously the effects of crowding and host plant nutrition on wing-form, I placed newly eclosed first instar nymphs of *P. **marginata*** at 5 densities on 2 different nutritional categories of caged *Spartina* seedlings and allowed them to develop to adults. The 5 densities were 1, 5, 10, 25 and 50 nymphs per cage (see Denno, Douglass and Jacobs, in press B for details). To achieve the two nutritional categories of plants, I chronically fertilized one bank of seedlings heavily and another bank lightly. Heavily fertilized plants contained 61.5 ± 7.4 $mg \cdot g^{-1}$ soluble protein, while lightly fertilized plants contained only 15.5 ± 4.3 $mg \cdot g^{-1}$. These nutritional and density categories span those commonly encountered in the field. Thus conditions that mimic high quality (low density on nutritional host plant) and low quality patches (high density on marginal host plant) were produced.

With increasing density on lightly fertilized *Spartina*, proportionally more adults molted to macropters (Fig 3). This pattern was not observed with animals raised on nutritionally superior seedlings, where at high densities, fewer macropters were produced. Apparently, the density-dependent migration response observed on marginal hosts is dampened when nymphs feed on more nutritious plants.

PATCH SELECTION BY PLANTHOPPERS

In the previous section it was shown that as environmental conditions deteriorate, long-winged forms that can escape are produced. Here I examine the ability of macropters to select and colonize more favorable host plants elsewhere and examine the fitness payoffs of this behavior. I tested nutritional preference on a small scale in the laboratory by placing 5 pairs of ***Prokelisia marginata*** in each of 10 small plastic tube-cages each containing one heavily fertilized seedling ($\bar{x}$ = 61.5 ± 7.4 $mg \cdot g^{-1}$ soluble protein) and one lightly fertilized seedling of *Spartina* ($\bar{x}$ = 15.5 ± 4.3 $mg \cdot g^{-1}$ soluble protein). Cages were kept in an incubator at 26°C. On six days during the following 2-wk period, the total number of planthoppers feeding on each culm were scored, and at the end of the 2-wk period the number of eggs per culm were counted. There was a very strong preference for heavily fertilized culms. The cumulative densities and loads (number of planthoppers per gram *Spartina*) of both feeding adults and eggs were significantly greater on heavily fertilized compared to lightly fertilized seedlings (Fig 4). While this experiment indicates the ability of planthoppers to discriminate and choose nutritionally superior hosts on a small scale, it does not pertain to long-distance colonization and patch selection.

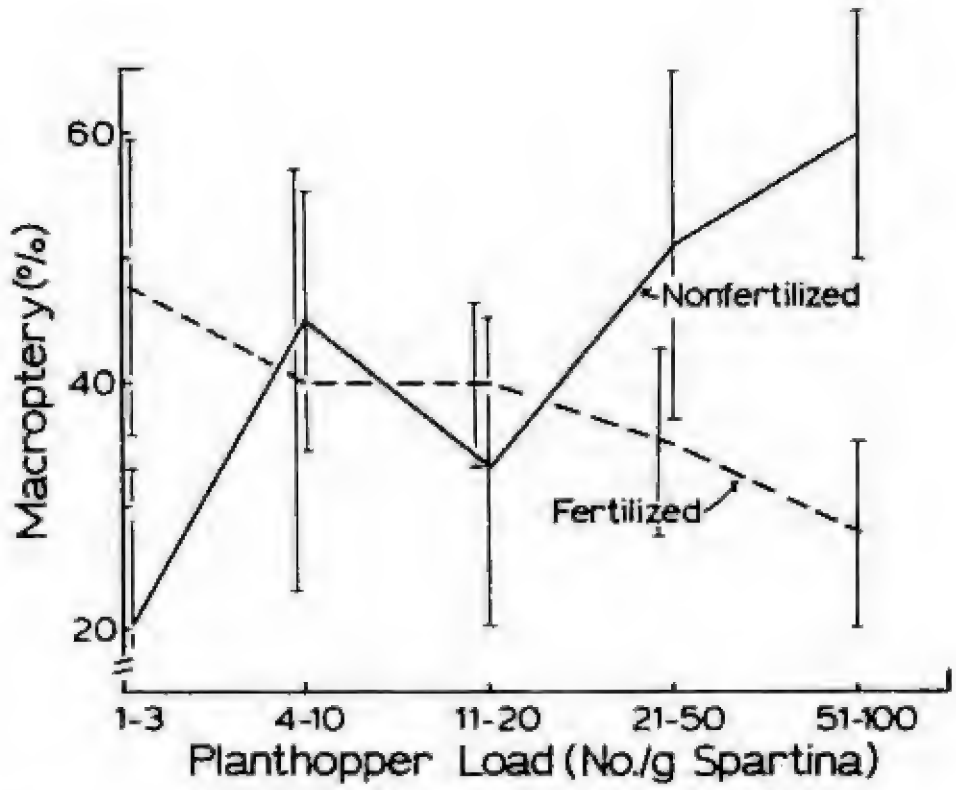

Figure 3

Relationship between macroptery (%) in eclosing adults of ***Prokelisia marginata*** and the degree of crowding (= planthopper load, number per gram ***Spartina***) incurred as nymphs on heavily fertilized and lightly fertilized seedlings of ***Spartina alterniflora***. Standard errors surround means.

On a larger scale in the field, Denno (1983) tested the ability of ***Prokelisia*** to select high quality patches of ***Spartina*** by the following experiment. Two, 100 m^2 field plots were chronically defaunated with biweekly applications of the short-lived, systemic insecticide, Orthene. Orthene has a half-life of about 5 days in the plant. Consequently, reproduction and development on the grass were drastically reduced, but colonization and selection by adults were not much affected during the last half of the 2-wk sampling interval when plants were not toxic. Two other plots were both chronically fertilized and treated with Orthene. Thus colonization and patch selection by planthopper adults could be compared on high and low quality ***Spartina***. There were significantly greater numbers of macropters in the fertilized compared to nonfertilized plots suggesting that macropters selectively chose high quality patches over less favorable ones (see Figure 17 in Denno 1983). In contrast, brachypters were equally rare in both plots suggesting that because of their immobility they were unable to colonize either plot and consequently make large scale choices between patches.

Several benefits accrue to those insects which colonize nutritionally superior host plants. For example, the nymphs and brachypters of ***Prokelisia marginata*** achieve very high densities in fertilized compared to nonfertilized plots of ***Spartina*** (see Figure 16 in Denno 1983). Furthermore, Vince, Valiela and Teal (1981) have shown that females of ***P. marginata*** which have developed on fertilized field plots of ***Spartina*** are significantly larger in size than those sampled from nonfertilized grass. Thus the ability of macropters to select high quality patches in the field results in larger and consequently more fecund offspring.

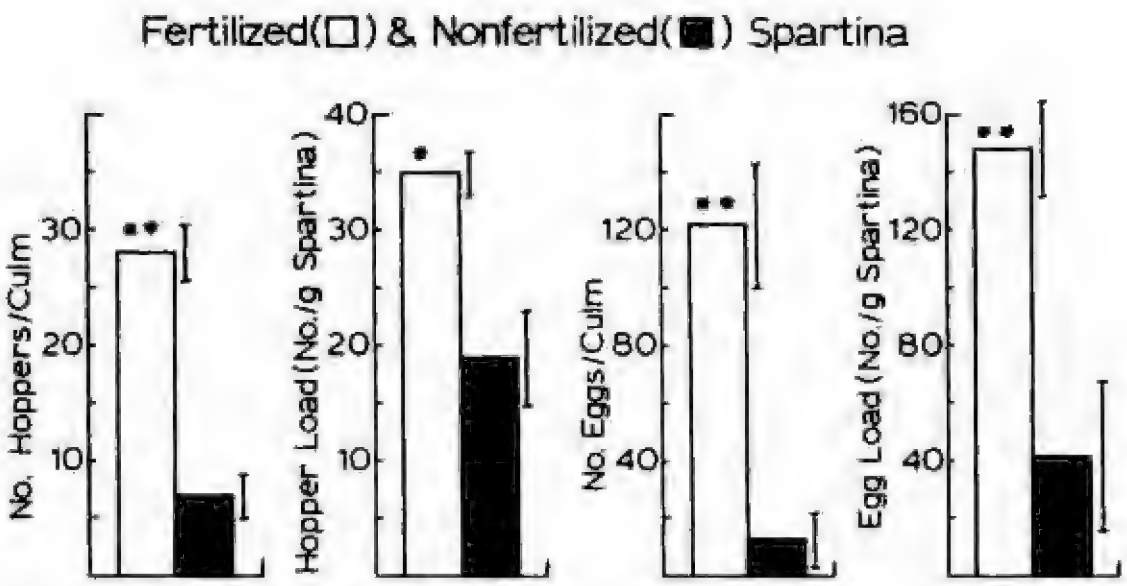

Figure 4

Feeding and oviposition preference of macropterous adults of ***Prokelisia marginata*** offered heavily fertilized ($\bar{x}$ = 61.5 ± 7.4 mg·g^{-1} soluble protein) and lightly fertilized $\bar{x}$ = 15.5 ± 4.3 mg·g^{-1} soluble protein) seedlings of ***Spartina alterniflora*** in a choice test. The densities and loads (number per gram ***Spartina***) of both feeding adults and eggs were significantly higher on heavily fertilized seedlings (Wilcoxon matched-pairs signed-ranks test, * = $p < 0.05$, ** = < 0.01). Standard errors surround means.

INTERHABITAT MIGRATION AND THE UNIQUE LIFE HISTORY OF *PROKELISIA MARGINATA*

The models of Southwood (1962, 1977) and Solbreck (1978) predict that for migration to be favored, alternative patches must be naturally available elsewhere and offer improved fitness potential for colonists (see Fig 1). If this were not the case, then diapause might be the only option when the local patch deteriorates. In this last section of my report I will show first that ***Spartina alterniflora*** occurs in two very different habitats, one which persists year-round and another that is only seasonally available, and secondly, that this host plant configuration has likely played a role in the evolution of the large commitment to migration in ***P. marginata*** (see Fig 1C).

On Atlantic coast salt marshes, ***Spartina alterniflora*** occurs as two dynamically different growth forms in two fairly discrete habitats (Denno and Grissell 1979, Denno et al. 1980, Denno 1983). Tall-form plants grow along the depressed borders of tidal creeks that run through the marsh. Here plants may reach 2 m in height during the summer. On the high, flat marsh near mean high-water level, short-form plants grow to only 10−40 cm tall. Short-form sprouts in spring, obtains maximum biomass in summer, dies in fall but remains standing through winter, and has associated with it a thatch where nymphs overwinter. Tall-form also sprouts in spring, obtains a very large, previously unexploited biomass in early summer, dies in fall, but due to the action of winds, waves and ice is knocked over and finally sheared off completely during winter leaving exposed creek banks which are unsuitable as overwintering sites for ***P. marginata***. Furthermore, because of the lower elevation of the creek bank habitat, plants remain inundated much of the time through spring. It is not until early summer that streamside vegetation grows tall enough for exploitation by planthoppers. While ***Spartina*** in the streamside habitat is certainly an ephemeral resource, it is more

nutritious during summer than is *Spartina* on the high marsh (Denno 1983).

Prokelisia marginata exhibits interhabitat migrations between high marsh and streamside vegetation (Denno and Grissell 1979). Nymphs overwinter on the high marsh and occur there in abundance throughout the year. Nymphs occur on streamside *Spartina* mainly during summer and fall. These nymphs are offspring of macropters that eclose on the high marsh and migrate to streamside vegetation in early summer. Nymphs on streamside vegetation molt primarily to macropters (conditions are very crowded) that migrate in the fall to the high marsh where they oviposit along with resident adults. The eggs that hatch develop into the overwintering population of nymphs. Colonization of the previously unexploited streamside *Spartina* in early summer results in tremendous populations of nymphs that molt to large adults. Planthoppers that remain on the high marsh at this time suffer the effects of crowding on a nutritionally inferior host as well as increased mortality due to growing populations of predaceous spiders (Denno 1983).

It is my contention that the 2-habitat configuration of *Spartina alterniflora* on Atlantic marshes has provided an opportunity for the evolution of migration in *Prokelisia marginata* and has been an important factor in shaping this insect's life history. For example, 81% of the adults of *P. marginata* are macropterous. This stands in direct contrast to the wing-form composition of all other known salt marsh-inhabiting planthopper species, where on the average only 6% of adults are macropters (Table 5). Unlike *Spartina alterniflora*, none of the host plants of these planthoppers occurs in two dynamically different habitats that provide the opportunity for interhabitat migration (see Fig 1A). Most are monotonous expanses of relatively uniform vegetation (e.g., *Spartina patens*, *Distichlis spicata* and *Juncus roemerianus*).

Perhaps even stronger evidence for the role that host plant heterogeneity plays in the evolution of migration comes when we examine wing-form patterns of the genus *Prokelisia* over a wide geographic range. *Prokelisia marginata* and its sibling congener *Prokelisia dolus* co-occur on *Spartina alterniflora* along both the Atlantic and Gulf coasts of North America (Wilson 1982). However, the structure and dynamics of *Spartina* are very different between the Atlantic and Gulf coasts. Reduced tidal range along the Gulf results in little contrast in structure between streamside and high marsh vegetation. Also, because of the equable climate, there is no evidence for the selective destruction of streamside vegetation. There is but one comparatively homogeneous stand along the Gulf coast where streamside and high marsh habitats are similar and available for exploitation all year. Here only 10% of the adults of *P. marginata* are macropterous (Denno and Grissell 1979, Denno 1983). *Prokelisia dolus*, which is restricted to the high marsh at Atlantic locations and fails to effectively colonize streamside vegetation, exhibits less than 30% macroptery in both Atlantic and Gulf coast populations (Table 5, Wilson 1982).

In summary, the life history of Atlantic coast *Prokelisia marginata*, where 81% of adults are macropters, is truly unique compared to other species of salt marsh planthoppers. I contend that it is the seasonal opportunity to exploit a vast ephemeral resource where fitness payoffs are high that has allowed for the evolution of migration

Table 5

Wing-morph composition of planthopper populations inhabiting salt-marsh vegetation.

Species	Host Plant	Location	Sample Size	% Macroptery
Delphacodes detecta	*Spartina patens*	New Jersey	23,868[c]	14
" "	*Spartina alterniflora*	New Jersey	16[a]	0
" "	*Spartina patens*	Maryland	84[a]	1
" "	" "	South Carolina	51[a]	0
" "	" "	Florida (Atlantic)	41[a]	17
" "	" "	Florida (Gulf)	51[a]	0
Delphacodes floridae	*Paspalum vaginatum*	Florida (Atlantic)	166[b]	12
" "	" "	Florida (Gulf)	56[a]	0
Delphacodes propinqua	*Distichlis spicata*	Florida (Gulf)	42[a]	14
Tumidagena minuta	*Spartina patens*	New Jersey	9,000[c]	1
" "	" "	Maryland	62[a]	0
Tumidagena terminalis	" "	Florida	13[b]	0
Neomegamelanus dorsalis	" "	New Jersey	58[a]	12
" "	" "	Maryland	50[a]	0
" "	" "	Florida (Atlantic)	63[a]	5
" "	" "	Florida (Keys)	41[a]	0
Neomegamelanus elongatus	" "	Florida (Gulf)	34[b]	26
Neomegamelanus penilautus	*Spartina spartinae*	Florida (Keys)	220[a]	1
Megamelus lobatus	*Spartina patens*	New Jersey	89[b]	3
" "	*Distichlis spicata*	New Jersey	73[a]	4
Megamelus trifidus	*Juncus roemerianus*	Florida	14[b]	0
Keyflana hasta	" "	Maryland	22[a]	0
" "	" "	Florida	12[b]	0
Pissonotus quadripustulatus	*Borrichia frutescens*	Georgia	39[a]	0
" "	" "	Florida (Gulf)	63[b]	0
" "	" "	Florida (Atlantic)	113[b]	0
" "	" "	Florida (Keys)	37[a]	0
Pissonotus albovenosus	*Iva frutescens*	New Jersey	9[a]	11
" "	*Borrichia frutescens*	South Carolina	29[a]	7
" "	*Iva Frutescens*	Florida (Gulf)	60[b]	7
Euides triloba	*Paspalum vaginatum*	Florida (Gulf)	23[a]	0
Prokelisia dolus	*Spartina alterniflora*	New Jersey	13,261[c]	29
" "	" "	Atlantic Coast	393[c]	16[d]
				$\bar{x} = 5.5 \pm 8.0$
Prokelisia marginata	*Spartina alterniflora*	New Jersey	42,606[c]	80
" "	" "	Atlantic Coast	424[c]	82[d]
				$\bar{x} = 81.0 \pm 1.4$

a; b; c = Samples from one season; samples from two seasons; and 1 year's data, at least bimonthly samples, respectively; d = From Wilson (1982).

in ***Prokelisia marginata*** (Fig 1C). The process is mediated by environmental cues like crowding and host plant nutrition that trigger a developmental switch to determine wing-form. This mechanism is not unlike the one for other planthopper species. Apparently with ***Prokelisia marginata***, selection has favored a low threshold of response; the developmental switch is very sensitive and the result is a high proportion of macropters that can actively colonize superior resources in distant habitats.

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INSECT MIGRATION STRATEGIES AND POPULATION DYNAMICS

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ABSTRACT

Insect migration by flight can be studied at several organizational levels. This paper deals with migration as an individual adaptation and as a process in population dynamics. Migration is a fairly complex behavioral process, and knowledge of the interplay between individual behavior and weather patterns is important for understanding migration as a population process. Using the large pine weevil, ***Hylobius albietis***, as an example, it is shown how even short duration flights may result in fairly extensive population movements by the insect because it takes advantage of winds high above ground. The scale of the spatial dimension of population dynamics is often underestimated, and too often population dynamics is studied in only one place on the presumption that this place represents population processes in general. Migration links different subpopulations and habitats which, when studied in isolation, may not necessarily represent large-scale population behavior.

Just as knowledge of the migratory process is fundamental to understanding population dynamics, knowledge of population dynamics is vital for assessing the adaptive significance of migratory behavior. However, it is only rarely known what factors actually affect the members of a population. The interactions may be complex, and often quite time consuming studies are needed to understand them. Using examples from two insects in Scandinavia, a seed bug ***Lygaeus equestris*** and a spruce bark beetle ***Ips typographus***, I try to illustrate the diversity of such individual-population-environment interactions.

INTRODUCTION

Insects can migrate in different life cycle stages and by rather different means, such as flight, ballooning on silken threads, walking, or by clinging to other moving objects. Having this variability in mind, however, one can nevertheless say that insects usually migrate as adults and by flight, and this is the kind of migration with which I will be concerned here.

Insect migration by flight is a phenomenon of great importance in several fields of biology, and an insect engaged in a migratory flight can be viewed by biologists in many different ways. It can be seen as a creature which has turned on a set of neurophysiological machinery, a moving body with navigational problems, or as an object moving genes around. Others could view it as a strategist exploiting a variable world to its best advantage, as a unit which changes population densities, or as an agent affecting the species richness of ecological communities. Insect migration is thus studied at several organizational levels, from cells to ecological communities, and questions are asked both with regard to migration as a mechanical process and as an adaptation. This paper is concerned with migration at two organizational levels, the individual and the population.

Migration by flight usually takes place during a distinct phase in the life of the adult insect, during which the insect is behaviorally and physiologically committed to flight while other functions such as reproduction tend to be suppressed (Johnson 1969). Accordingly, migration is an important life history trait coupled to other traits such as reproduction, and it is part of an adaptive life history syndrome (or migratory strategy) molded by the environmental "template" (Dingle 1972, Solbreck 1978, Southwood 1977). This individual migratory strategy will affect the dynamics of the population of which the individual is a part. However, the population also forms an important part of the biotic environment of the individuals, either directly or via its effects on food resources, enemy populations, etc. The connections between individual adaptive behavior and population dynamics are thus profound and reciprocal (Peterman, Clark and Holling 1979).

In the process of migration, behavior and population events are intertwined. In the words of Taylor and Taylor (1983), "Movement links the behavior of the individual with the biology of the population." To illustrate this point I will start by describing the process of migration in the large pine weevil (***Hylobius abietis***). The behavior of ***Hylobius abietis*** will be shown to be one example of a wide array of behaviors among insect migrants. Regarding distances traveled, there is also large variation between species, and ***Hylobius abietis*** can be seen as an example of the common "medium-range migrations."

In ***Hylobius abietis*** the habitat changes that favor migration are easily visualized. In many cases, however, a more detailed picture of habitat change and population dynamics is needed in order to evaluate how insect behavior and the environment interact. These problems are introduced in the section on "migration and the environmental template." Two case studies are then presented to further illustrate the interplay between migration and population dynamics.

The first case considers a distasteful bug, ***Lygaeus equestris***, which represents a population system where effects of natural enemies are insignificant (Sillén-Tullberg and Solbreck, in preparation). Migratory habits and population dynamics are mainly affected by spatial and temporal variation in food resources and microclimatic conditions.

The other case deals with a bark beetle, *Ips typographus*, that is not just dependent upon this resource template but which severely interacts with and modifies its resource base. It also suggests that enemies can be important in affecting the suitability of habitat patches.

Both these examples further illustrate that there is a need for long-term field studies to understand population dynamics and thus to evaluate what selective forces shape migratory strategies.

This presentation is not intended to be a general review article, but I have chosen to use examples mainly from my own work and that of some colleagues.

THE PROCESS OF MIGRATION

Migration is a complex process, and its duration and the way it is undertaken are highly variable. Several review articles have dealt with the various factors that affect the recruitment of presumptive migrants or upon the proportion of long flights in laboratory experiments (e.g., Dingle 1979, Harrison 1980, Johnson 1976). Less emphasis has been devoted to studying the behavior of the migrant all through the migratory process. Notable exceptions are the studies on the black bean aphid (Kennedy 1974). Information is also scanty with regard to how insect behavior and weather conditions interact to produce patterns of movement, although there are notable exceptions in studies on some insect pests such as locusts, armyworm moths (e.g., Betts 1976, Rainey 1978, Riley, Reynolds and Farmery 1983) and the spruce budworm (Greenbank, Schaefer and Rainey 1980).

The usual problem with studying migratory behavior under field conditions is that almost as soon as the insect behaves, it is lost to sight. Migration paths thus have to be tracked by putting together information from different types of studies. Radar studies (Schaefer 1976) have been a vital ingredient in some, but with insects that are relatively rare in the air or which fly inside forests, problems of identification and tracking tend to become insurmountable.

Migration has been studied predominantly in insects that are of economic importance and thus are common, and that occur in agroecosystems. Insects that are rare or moderately common, or that occur in forests, are strongly underrepresented. I will use an insect in the latter category, the large pine weevil ***Hylobius abietis L.***, to illustrate the duality of migration as both a behavioral and population process.

Hylobius abietis is an insect of economic importance in northern Europe due to the damage done by the feeding adults to the bark of young conifer plants (Eidmann 1979). During June, beetles oviposit on the roots of newly cut or otherwise recently killed conifers. The larvae feed under the bark of the roots and, depending upon latitude and local microclimatic conditions, they will develop into new adults in one to four years (Eidmann 1974). By the time the adults emerge, the local food base for the larvae has largely disappeared due to insect feeding or other causes. Thus beetles have to fly to new localities to find suitable oviposition sites in every generation (Eidmann 1977). Migration by flight is accordingly an important process in the population dynamics of this species.

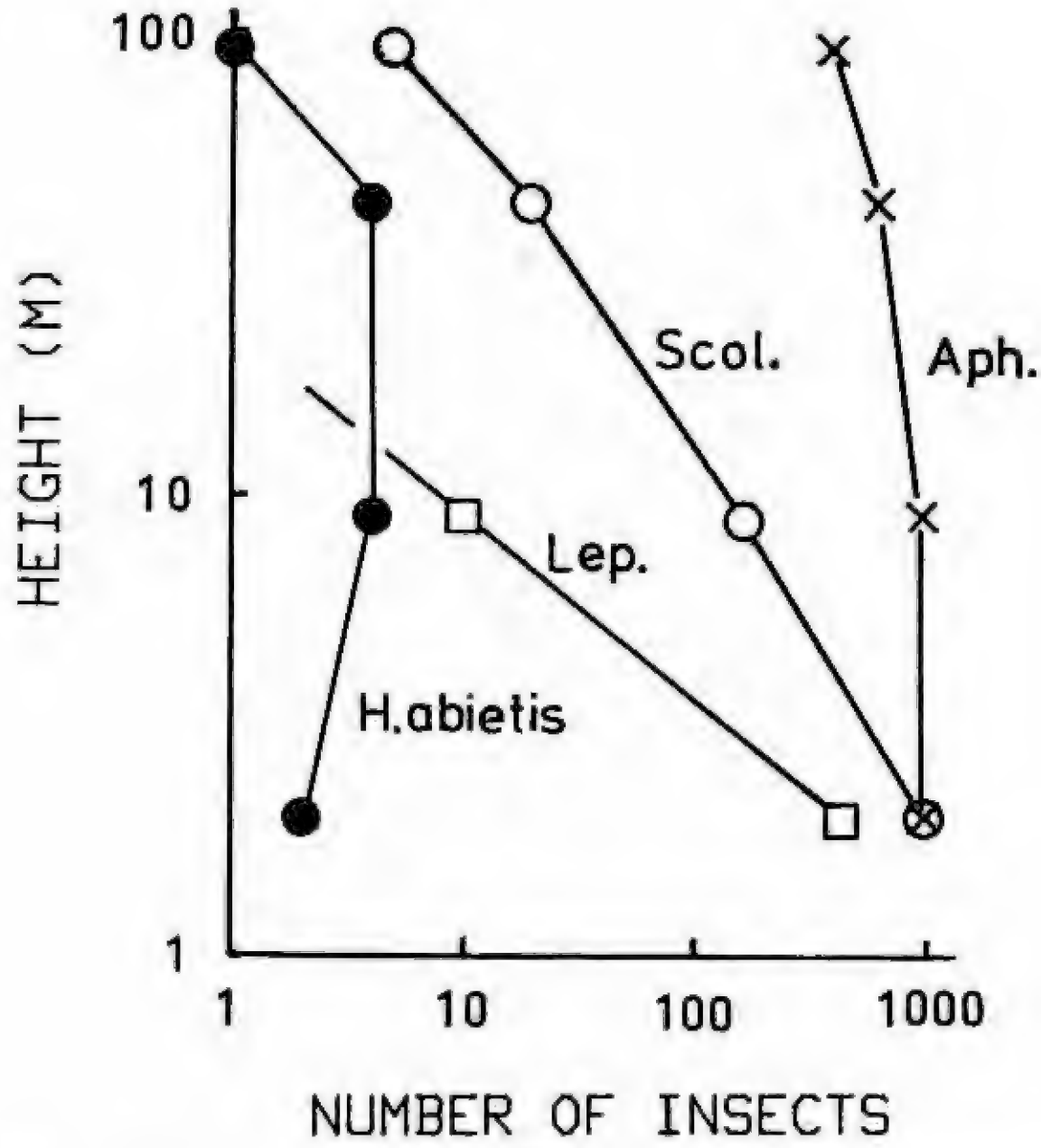

Figure 1

Density-height profiles of *H. abietis*, Lepidoptera, Scolytidae and Aphidoidea above an old clear-cut area in a mixed coniferous forest area in west central Sweden. Total suction trap catches for the period 1–12 June, 1980.

In central Sweden, pine weevils migrate during one to two weeks in late May to early June, when temperatures are above 16–18°C and wind speeds are low (Solbreck and Gyldberg 1979). When they take off in their natural habitat, beetles always face the wind, but within seconds they turn their body around and fly downwind. Most beetles also fly upwards for as long as they can be followed, a behavior which results in most pine weevils migrating high above the forest canopy (Solbreck 1980). This is illustrated by the steep density-height profile of pine weevils obtained by suction trap catches on a TV tower in Sweden (Fig 1). Although the sample of ***Hylobius abietis*** is small, its profile is certainly more similar to that of aphids, a group of insects generally regarded as typical representatives of the so-called aeroplankton, than to scolytids which show a profile typical of most beetle groups in this geographical area (Solbreck, unpublished).

How far will these flights take the beetles? From suction trap catches at a saw mill (where densities of flying weevils are high) a measure of the frequency of flights at different wind speeds was obtained. Using this frequency distribution and measures of the mean air speed of pine weevils flying in the field (1.9 $m \cdot s^{-1}$), a distribution of dispersal speeds (or ground speeds) in a pine weevil population could be calculated. This was further corrected by taking into account the increased windspeeds at an assumed mean height of flight of 30 m (which probably is too low) above ground (Solbreck 1980).

In order to estimate dispersal distances, a measure of flight duration was also needed, and this was obtained from laboratory studies on flight mills. Both flight duration per day (Fig 8) and total flight duration over the entire flight period (which lasts 1−2 weeks) were measured. Flight times on flight mills are not necessarily the same as those under field conditions, but in this case they seem to give a rough measure of flight potential (Solbreck 1980). Insects flying in the field may interrupt their flights earlier if they reach suitable places. Flying pine weevils evidently respond to odors from wounded conifer trees since they accumulate around saw dust heaps at saw mills. There they can be seen flying steeply downwards or against the wind.

Potential dispersal distances (per day or for the entire flight period) were calculated by multiplying flight time and dispersal speed distributions. This showed, for example, that 10% of an ***H. abietis*** population can travel more than about 10 km per day or 50 km for the entire flight period (Fig 2) (Solbreck 1980). Thus ***H. abietis*** populations, despite the relatively short duration flights, are quite mobile. One practical consequence of this finding is the suggestion that population management efforts for this species probably should be coordinated on a much larger spatial scale than previously supposed.

The flight of an individual pine weevil seems to consist of three phases. First, beetles fly towards the sky to gain height. This is followed by a transport phase when the beetle traverses the landscape at the combined speed of the wind and its own flight. Then follows a phase when the insect responds to host odors by moving down and upwind. Another important aspect of flight behavior is that the beetle often makes many flights over several days. It can therefore land and "evaluate" different habitat patches. Thus the insect migrant does not have to find its new habitat in a single hazardous flight; it can try repeatedly.

How typical is ***H. abietis*** migration of insect migration by flight in general? Among insect migrants, there is considerable variation in flight altitude. While some insects have a large proportion of their populations at high altitudes, others, like many Lepidoptera, tend to fly much closer to the ground (Fig 1). This allows them to better control their flight direction, in relation to the points of the compass, than do insects like ***H. abietis*** with wind-aided flights high above the forest canopy. In the case of ***H. abietis*** there are no reasons for traveling in any preferred compass direction since new breeding resources are just as likely to occur in any direction. Riding on the wind evidently allows the beetle to scan larger areas for new breeding sites.

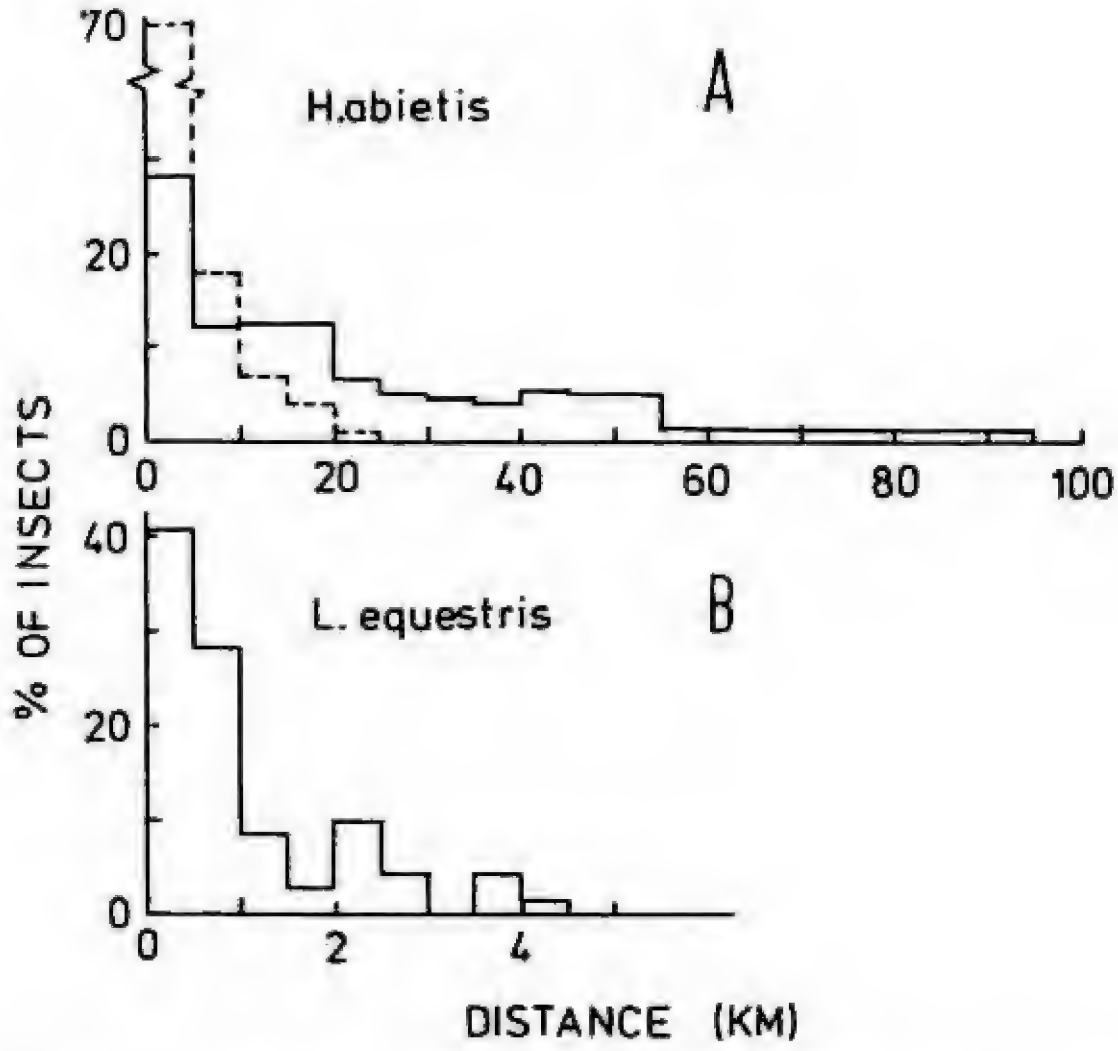

Figure 2
Estimated dispersal distances of two insects. (A) Potential dispersal distances calculated for *H. abietis* females per day (broken line) or for the entire migration period (after Solbreck 1980). (B) Dispersal distances of *L. equestris* during the fall migration based on recaptures of marked individuals (after Solbreck 1971).

With regard to distances traveled, there are also large variations among insects. Some insects such as the monarch butterfly (several papers, this volume) make very long, continent-wide migrations. In other cases, however, migrations can be very short, as in the lygaeid bug *Lygaeus equestris*, where most individuals fly from a few hundred meters to several kilometers (Solbreck 1971) (Fig 2). In comparison with the short-range flights of *L. equestris*, the migrations of *H. abietis* are evidently on a somewhat larger scale and may be called medium-range migrations. It seems that most insect migrants, with regard to distances moved, fall in these short and medium-range categories. Taylor and Taylor (1983) also pointed out that great distance is not typical of most migration movements.

Most insects migrate during a limited phase of the life cycle and display a specialized behavioral sequence aimed at taking the individual away from its place of origin and onto one or more journeys, the goal of which is not perceived at the start of the flight. This individual behavior has important effects on the dynamics of the population. Thus the population of *H. abietis* in a new clear-cut area increases rapidly and manifold in early summer mainly due to immigration, and the decrease in the same locality one generation later is largely due to flights of emigrants to new breeding sites. Although most migrations, as in *H. abietis*, are probably on a

moderate scale (1−100 km?), this scale is nevertheless very large to consider in practical field studies. This problem has to be addressed, however, since spatially limited studies cannot safely be thought of as representing population dynamics over larger areas where local extinction and recolonization may be common events (cf. den Boer 1982; Taylor and Taylor 1977, 1983).

MIGRATION AND THE ENVIRONMENTAL TEMPLATE

In the case of *H. abietis* it is evident that weevils that stay where they grew up will have a low probability of finding suitable breeding sites. In every generation, beetles have to move to new patches where storms, forest fires or, in the modern forest, logging practices have created fresh resources for breeding. In *H. abietis*, as in many other insects, migration thus seems to be an adaptation to exploit ephemeral habitats (Southwood 1962).

Migration is, however, not the only possible mechanism by which insects might survive in a temporary environment. They can, for example, enter a dormant state such as diapause. The analogies between diapause and migration were pointed out long ago by Kennedy (1961). Thus migration and diapause can be seen as ways to bridge "gaps" in space and time respectively. Whether diapause or migration is favored depends on patterns of change in ***both*** time and space. Migration seems to be selected for when environmental changes are asynchronous, while synchronous changes tend to favor diapause (Gadgil 1971, Solbreck 1978). To understand migration strategies we thus have to consider in more detail what specific kinds of habitat change are taking place (cf. Southwood 1977). One must take into account not only environmental changes in the place where the insect presently lives, but the relative favorability of habitats "here" and "elsewhere" (Solbreck 1978). Migration can thus be favored even for an insect living in a very stable and suitable habitat if habitats elsewhere become even more favorable.

There has been a tendency to regard insect migration primarily as an adaptation for tracking changes in food resources or of coping with seasonal climatic changes, but usually only crude measures of how these factors vary are available (Solbreck 1978, Harrison 1980). Regarding the role of other environmental factors such as natural enemies, even less is known, although they could be very important for the selection of migration in many cases (Southwood 1978). One also must consider that insect populations are usually affected by a complex web of interactions (Clark, Geier, Hughes and Morris 1967; Schwerdtfeger 1941). Thus in his article "Habitat, the template for ecological strategies?" Southwood (1977) used a question mark at the end of the title to warn against a view of the environment as a rigid causal template. Often one has to consider reciprocal interactions between the insect and its environment. The life history of the insect will, for example, affect the growth of the population, which will affect the environment and thus in turn the selective pressures from the environment on the individual.

A serious practical problem in understanding migratory strategies, is that we rarely have a thorough knowledge of what population processes are important in each specific case. What are the roles of specific food items, predators, competitors, parasitoids, parasites, pathogens or weather conditions and how do these interact? To solve these kinds of questions requires quite time-consuming studies.

MIGRATION STRATEGY AND POPULATION DYNAMICS—TWO CASE STUDIES

Lygaeus equestris

The bug ***Lygaeus equestris*** (L.) (Heteroptera, Lygaeidae) feeds on the green ovulae or seeds of ***Vincetoxicum hirundinaria*** Medicus (Asclepiadaceae). ***Vincetoxicum hirundinaria*** is a perennial and very longlived herb that on mainland Sweden grows on rocky escarpments or at forest edges and has a very patchy distribution. Patches of the plant are virtually the same from year to year so, as a habitat, these plant islands are very stable indeed. ***Vincetoxicum hirundinaria*** flowers abundantly every year, but pod production varies by a factor of about 100 from year to year, mainly due to drought in the open rocky habitats (Solbreck and Sillén-Tullberg, in preparation).

Lygaeus equestris overwinters as an adult in crevices in rock walls in sun-exposed positions. These hibernation sites, where hundreds or thousands of bugs may aggregate, are sometimes close to breeding sites in ***Vincetoxicum hirundinaria*** patches. Often, however, they are hundreds of meters or a few kilometers away from breeding sites. In the fall the bugs migrate by flight to these hibernation sites, and in the spring they fly again to colonize ***Vincetoxicum hirundinaria*** patches for breeding (Solbreck 1971, 1976). Normally only one offspring generation is produced during the summer at these localities (Solbreck and Sillén-Tullberg 1981).

In late June we estimated populations of parent bugs by mark-recapture techniques. The same was done in August, when their offspring had become adults, but before they had reached the development stage that migrates to hibernation sites. Hibernating populations were also estimated by the same method in April before the spring migration. In this way local populations were followed over seven years in over forty ***Vincetoxicum hirundinaria*** patches (in two study areas).

Lygaeus equestris is a distasteful insect, and it has no natural enemies in these areas. Accordingly we expected that populations were food limited. Much to our surprise, several years of correlational data could not establish any significant relationship between seed crop and concomitant population growth rate. However, there was a significant correlation between seed production and population growth rate of ***Lygaeus equestris*** the following year. This suggested that dry seeds on the ground from the previous year are the limiting resource (Sillén-Tullberg and Solbreck, in preparation). This conclusion was supported by field experiments (Fig 3). So what one usually observes the insect to feed on in the field (flowers and pods) is usually not the critical resource; it is rather what they feed on when they are hidden by debris on

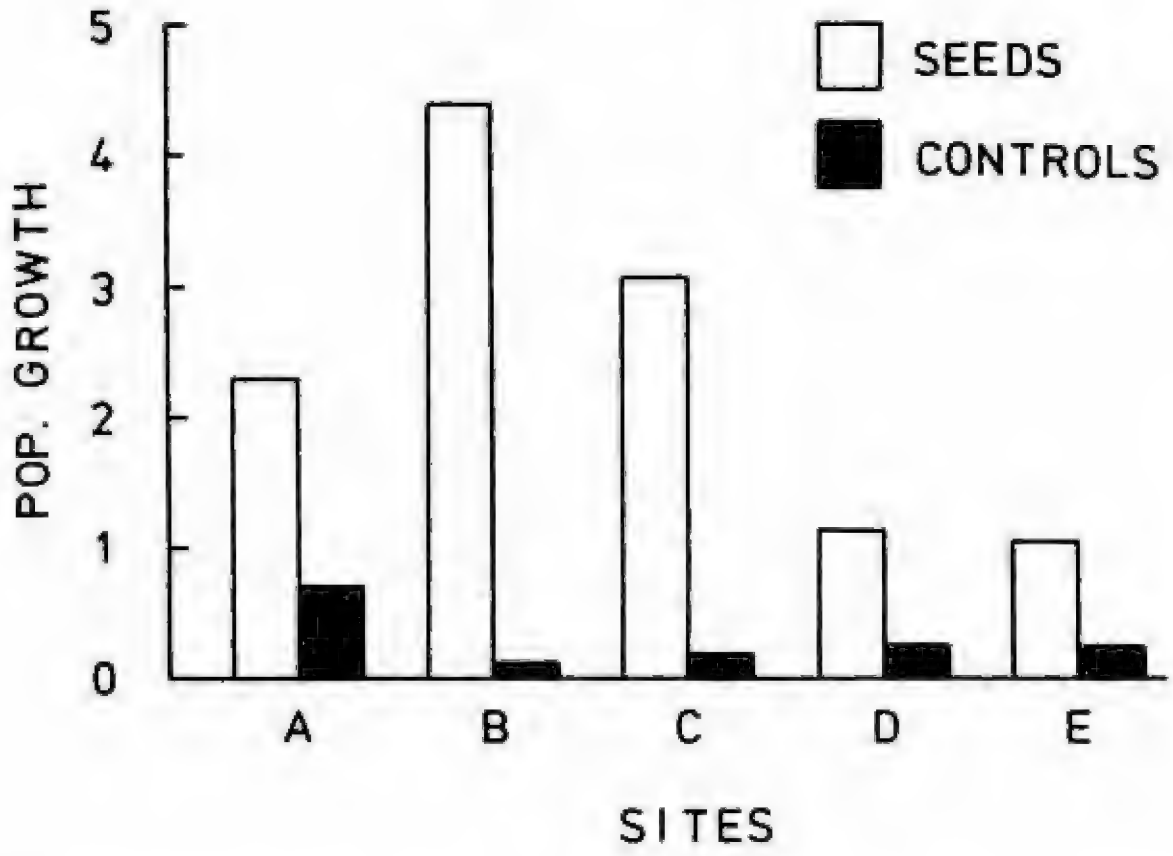

Figure 3

Effects of added seeds on the ground on population growth (adult offspring/parent) of *L. equestris* in five pairwise experiments in natural habitats.

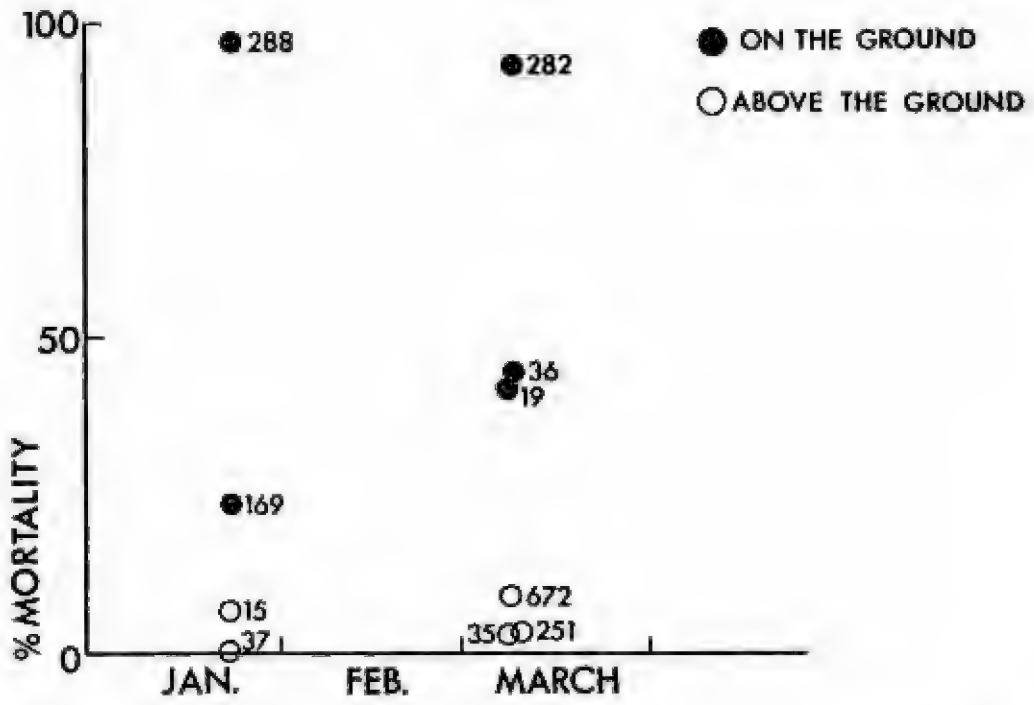

Figure 4

Mortality of *L. equestris* (on Gotland 1974) when hibernating on and above the ground. Numbers show sample sizes.

the ground. Several years of field studies were needed before the right question could be asked and the simple critical field experiment performed.

Seed production varies much between host plant patches. Furthermore, the relative production of each patch varies between years (Solbreck and Sillén-Tullberg, in preparation). These patterns are largely determined by weather and edaphic factors. Another important aspect of this insect-environment interaction is that most host-plant habitats are not suitable for hibernation. Bugs on the ground suffer heavy mortality compared with those that move to ordinary hibernation sites such as crevices in steep rock walls (Fig 4). There is accordingly a complicated pattern of within and between habitat variation, to which the insect must gear its migratory habits.

During the spring migration, bugs fly and colonize host plant patches. The result of this is exemplified in Figure 5, which shows what is happening during one season (1983) in part of one of our study areas. During hibernation, bugs occurred at ten sites, mainly on rock walls. In mid-June the same bugs appeared in 19 of the 21 host plant patches of this area. Some were close to hibernation sites, while others were several hundred meters away. Marking experiments confirmed that bugs had flown between these places (Sillén-Tullberg and Solbreck, in preparation) (cf. Fig 2).

The colonization of the host plant patches is a gradual process during May and part of June. The bugs make many flights and "evaluate" their landing places. Females lose their flight ability as they feed and become heavy with eggs. Thus females tend to stay in habitats where food is abundant. Females that reach poorer habitats continue to fly. This is demonstrated by the high frequency of empty stomachs among females that are flying during the breeding period and by the finding that females deprived of food respond with increased take off activity in laboratory experiments (Fig 6).

Males retain much of their flight ability during the breeding period. However, they also respond to food abundance by decreasing their willingness to take off (Fig 6). Another important factor that lowers the likelihood of flight is the occurrence of mates. Copulations last for very long periods in *L. equestris* (up to 24 hours), and they are often repeated (Sillén-Tullberg 1981). Thus the occurrence of mates will also reduce take-off rate (in both sexes).

What are the population losses during this extended migration period? We have data for five years to compare late April populations at hibernation sites with breeding populations in host plant patches in June (data from one entire study area of about 20 km^2). Mortality averaged 49.6% for this period, but most of this is undoubtedly due to other causes than migration. Although these findings cannot say much about the cost of longer flights, they do not suggest that migration in general is costly in this population (almost all bugs migrate, although some fly very short distances).

The outcome of reproduction varies much between habitat patches (Fig 5B). Most subpopulations increased this year but some were constant, and some even decreased. The preceding year had a low seed crop, and the breeding population was rather high in June 1983. This was a year when one would expect intraspecific competition to be important. Many marked bugs were recovered this year, and it may be possible to determine the relationship between migration distance and reproductive success in the colonized habitat patch during a year when competition is severe (Fig 7).

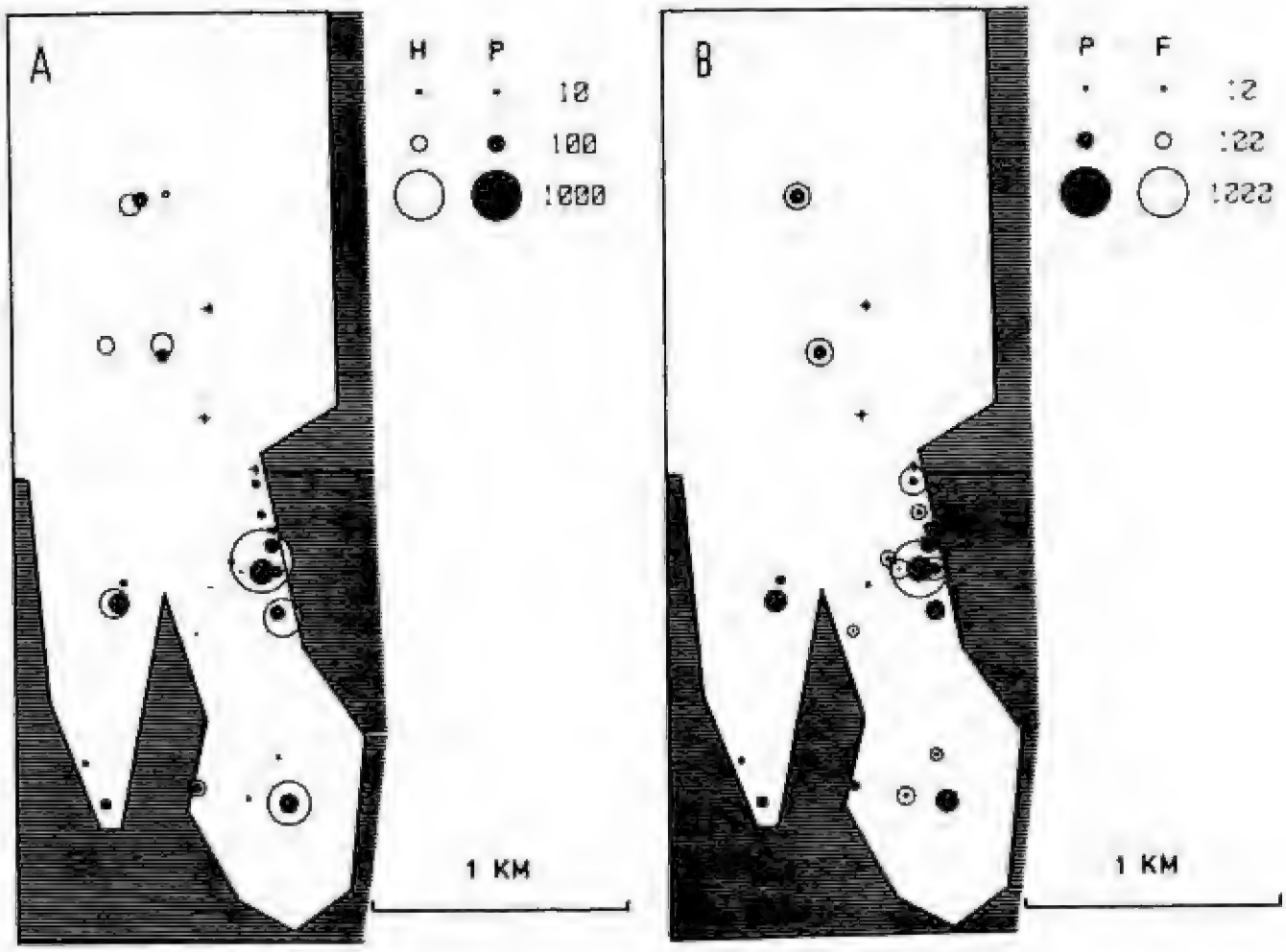

Figure 5

Changes in population sizes of *L. equestris* subpopulations at Tullgarn, Sweden 1983. Circle area is proportional to population size. The habitat patches are rather small, ranging in size from 1 to 170 m^2.
A. Populations of parent bugs at hibernation sites in April (H) and in host plant patches in June (P).
B. Populations of parent bugs in June (as in A) and of their adult offspring in late August (F). Crosses denote empty patches.

Bugs that had moved less than 100 m never realized a growth rate of over 6, but in the group of bugs that had moved farther, there was much more variation in reproductive success. Because of problems in deciding which observations are independent in this sample, it is difficult to make a formal statistical analysis of these data. However, some of the bugs flying farther than 100 m had a considerably higher fitness (up to ten times) than those staying close to hibernation sites. These are evidently the bugs that happened to colonize the host plant patches where intraspecific competition was low.

To summarize, migration in this insect is undoubtedly a trait subjected to extreme variations in selection pressure both within and between years. Migration enables *L. equestris* individuals to survive the winter by choosing particular microclimatically favorable sites. It also enables bugs to exploit small and isolated habitat islands where they can often reproduce at a higher rate but where they would have difficulty surviving all through the year. The migratory habit in this meta-population can be explained as a problem of tracking food resources, avoiding intraspecific competition and exploiting micro-climatically favorable sites (Sillén-Tullberg and Solbreck, in preparation).

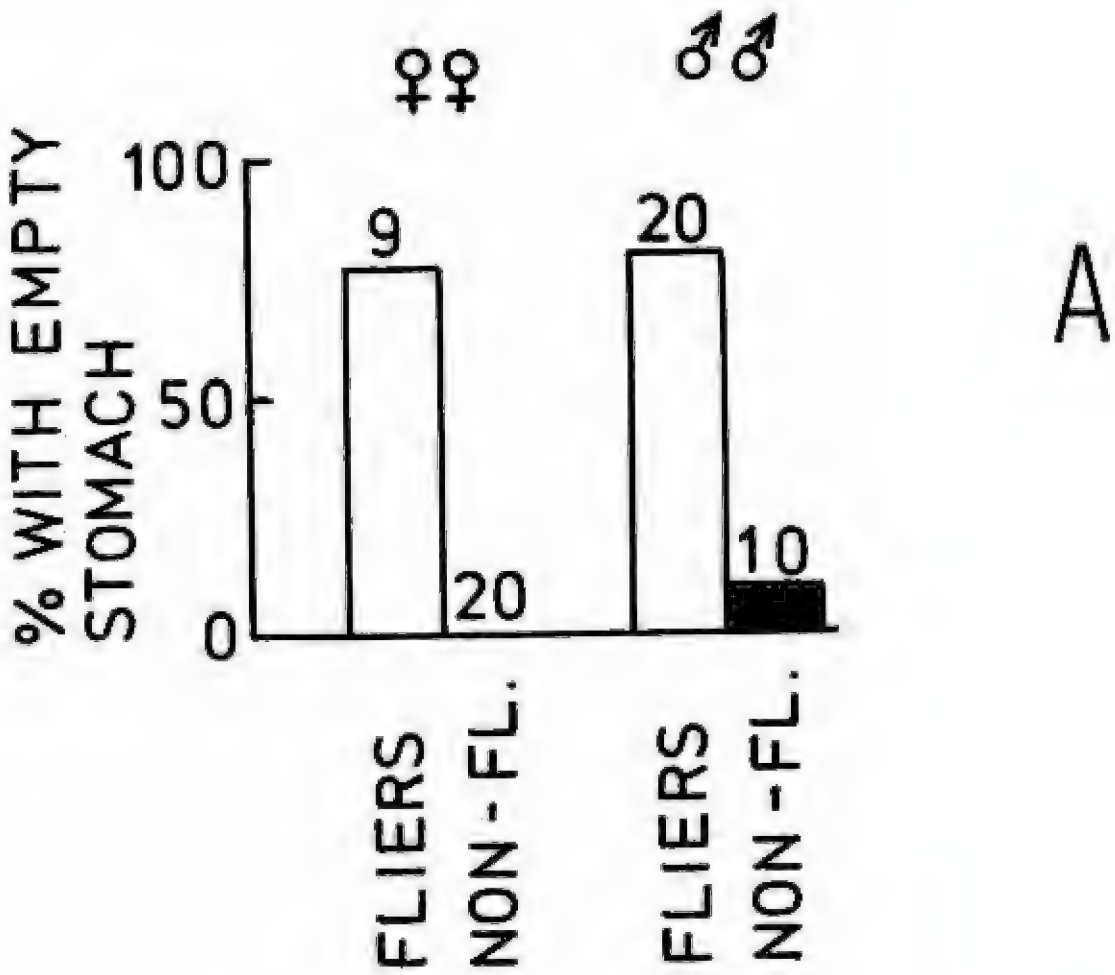

Figure 6

Effects of food on flight in *L. equestris* during the end of the spring migration period. (A) Percent of field-collected, flying bugs with and without food in the stomach. Differences are significant for both sexes separately ($p < 0.001$, one-tailed Fisher exact test). (B) Take-off rate of fed (sunflower seeds) and starved bugs in laboratory experiments. Bugs were kept at 18°C for 20–30 days following the start of the spring migration period. Differences are significant for both sexes ($p < 0.001$ and $p < 0.05$ respectively, one-tailed χ^2 test). Numbers above bars show sample sizes.

Ips typographus—The Spruce Bark Beetle

This is another forest insect of great economic importance in Scandinavia. Damage occurs during periods of mass outbreaks when beetles attack and kill standing, healthy spruce trees (Bakke 1982, 1983). The beetle overwinters in forest litter or logs and starts to fly in May in Sweden. Beetles fly in search of suitable breeding material, which is freshly fallen spruce logs, or—under epidemic conditions—standing trees. Males bore into the bark and attract females as well as other males by emitting pheromones (Bakke and Riege 1982). They then mate and start constructing egg galleries.

When the beetles attack standing trees, they can only overpower and kill the tree if they attack in large numbers, about 600 per m^2 of bark surface (Regnander, personal communication). Although this threshold certainly varies with tree vigor, it is nevertheless appropriate to divide the breeding resources of *I. typographus* into two broad categories, "fallen trees" that can be used by the beetles also at low densities and "standing trees" which can only be overpowered if they are attacked by beetles at high densities. Densities high enough to overpower standing, healthy trees mainly occur in the immediate surroundings of previously attacked trees. In succeeding years, following an initial outbreak, fewer and fewer standing trees are killed in such a *local* forest patch, and after about five years the local attack has usually faded away (Bombosch 1954, Lekander 1972).

If beetles are flight tested in the laboratory during this spring flight period, many will show a considerable flight capacity. Beetles can fly day after day for as long as one cares to test them. The only requirement is that they are given small amounts of spruce bark, which allows feeding but not gallery construction. Beetles deprived of food are also able to make extensive flights but only during a couple of days (Forsse and Solbreck, in press).

The flight potential per day is also considerable. A large proportion of the beetles fly for more than one hour (Fig 8). This is much more than the pine weevils do. Field observations also show that beetles sometimes fly considerable distances under field conditions (Botterweg 1982, Nilssen 1978). The closely related species *Ips amitinus*, which has been extending its range in Finland lately, has been shown to have a rate of spread of about 20 km per year (Koponen 1980). The spruce bark beetles can thus scan extensive forest areas if needed, in search of suitable breeding material. This migratory potential seems a little odd if one only considers outbreak conditions. During normal conditions, however, beetles breed in newly fallen trees, a resource which is highly temporary and scattered through the forest.

When beetles start to construct galleries they lose their flight ability, but it is regained after gallery construction is completed (Forsse and Solbreck, in press). Many beetles then fly a second time to breed in a new log or tree (Bakke 1983). During this second flight period, flight potential—at least per day—is as high as during the first flight period. Some beetles, perhaps 10%, hibernate a second time and migrate again

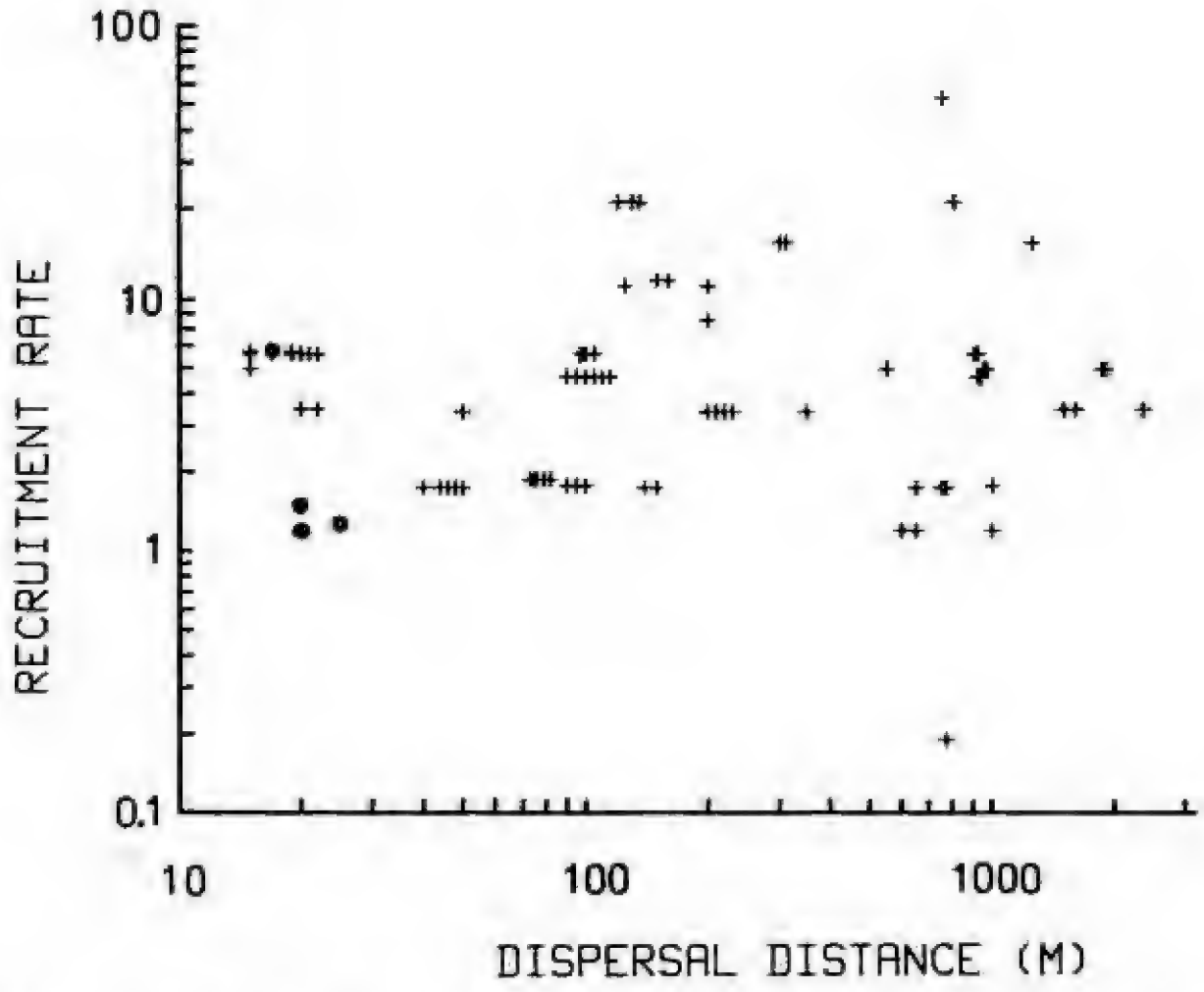

Figure 7
Recruitment rate (adult offspring/parent) for *L. equestris* parents making spring migrations of different lengths at Tullgarn 1983. Filled circles denote more than ten individuals. Notice log scale on both axes.

the following year. It is, however, unknown whether or not these beetles were engaged in full migratory and reproductive activity the first year.

Why do these beetles fly so far in search of fallen trees when they can breed in standing trees only a couple of meters away? To understand this one has to look into the dynamics of *I. typographus* populations in fallen versus standing trees.

Let us start by looking *only* at the role of intraspecific competition in a log. As the density of parents increases there is a decrease in per capita egg production. There is also an increase in larval mortality due to intraspecific competition (Ogibin 1974a, Thalenhorst 1958). Thus the per capita replacement rate decreases from around twenty daughters per mother at low density to below one at high densities (Fig 9).

If beetles attack a standing, healthy tree, attack density has to be above a certain threshold in order to kill the tree. Therefore the replacement rate in standing trees is always low (Fig 9).

When beetles are attacked by natural enemies, and the spruce bark beetle has a large number of predators and parasitoids (Thalenhorst 1958), the replacement curves will be pushed downwards. Thus it becomes evident that beetles in standing trees will have great difficulty in achieving a replacement rate above one. It is typical that once an outbreak has started, the number of killed trees usually remains constant or decreases from year to year. If increases occur, they are rarely more than twofold (cf. Bakke 1983, Bombosch 1954, Lekander 1972).

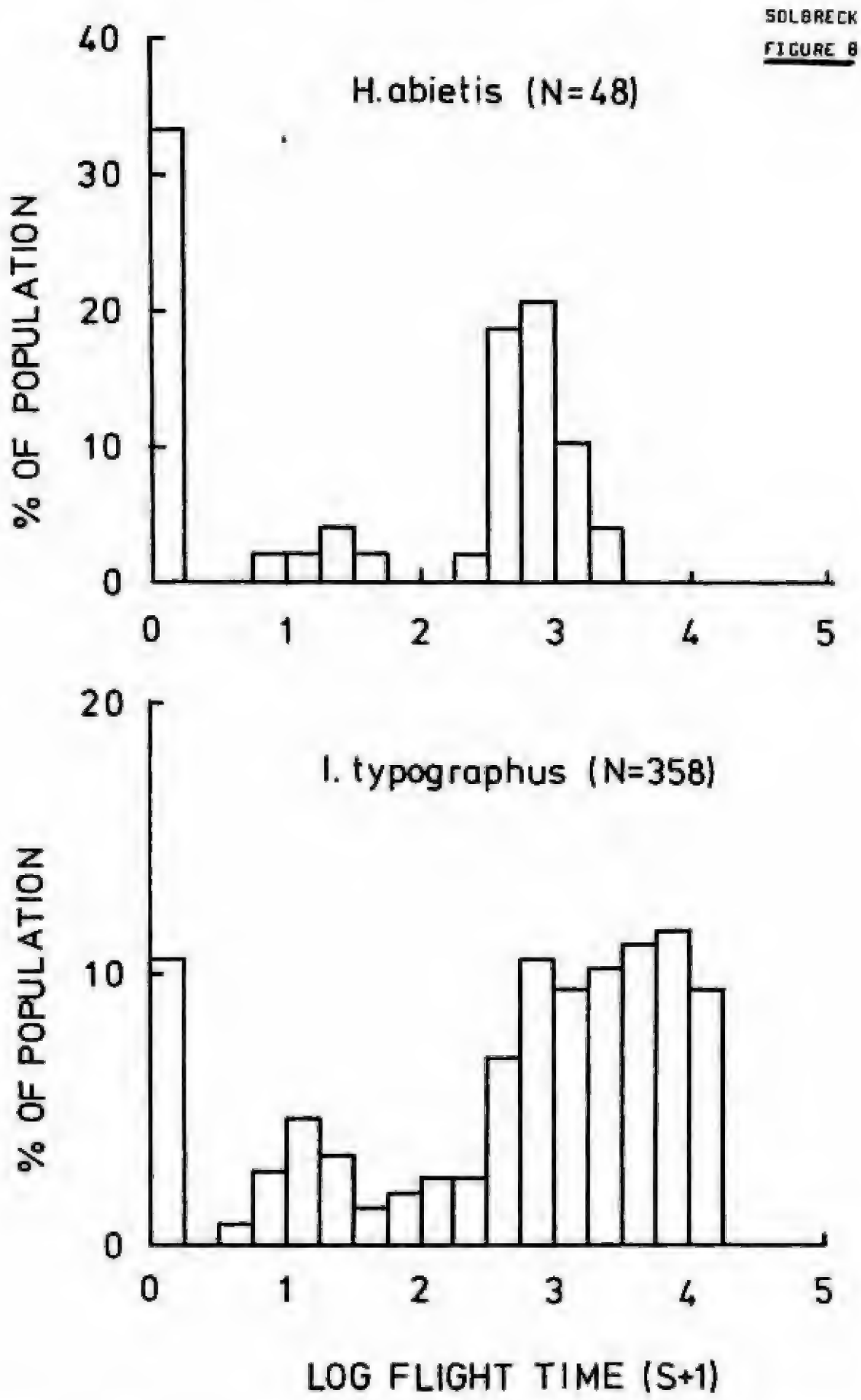

Figure 8

Flight duration (log (seconds + 1)) distribution of *H. abietes* and *I. typographus* tested on flight mills during one day of the spring migration period (from Solbreck 1980 and Forsse and Solbreck, in press).

There seems to be no density-dependent response in the effects of natural enemies in logs with different densities of bark beetles (Ogibin 1974b). However, the density of enemies nevertheless increases in successive years when there is an outbreak in a local patch of standing trees (Thalenhorst 1958). Added to the effects of

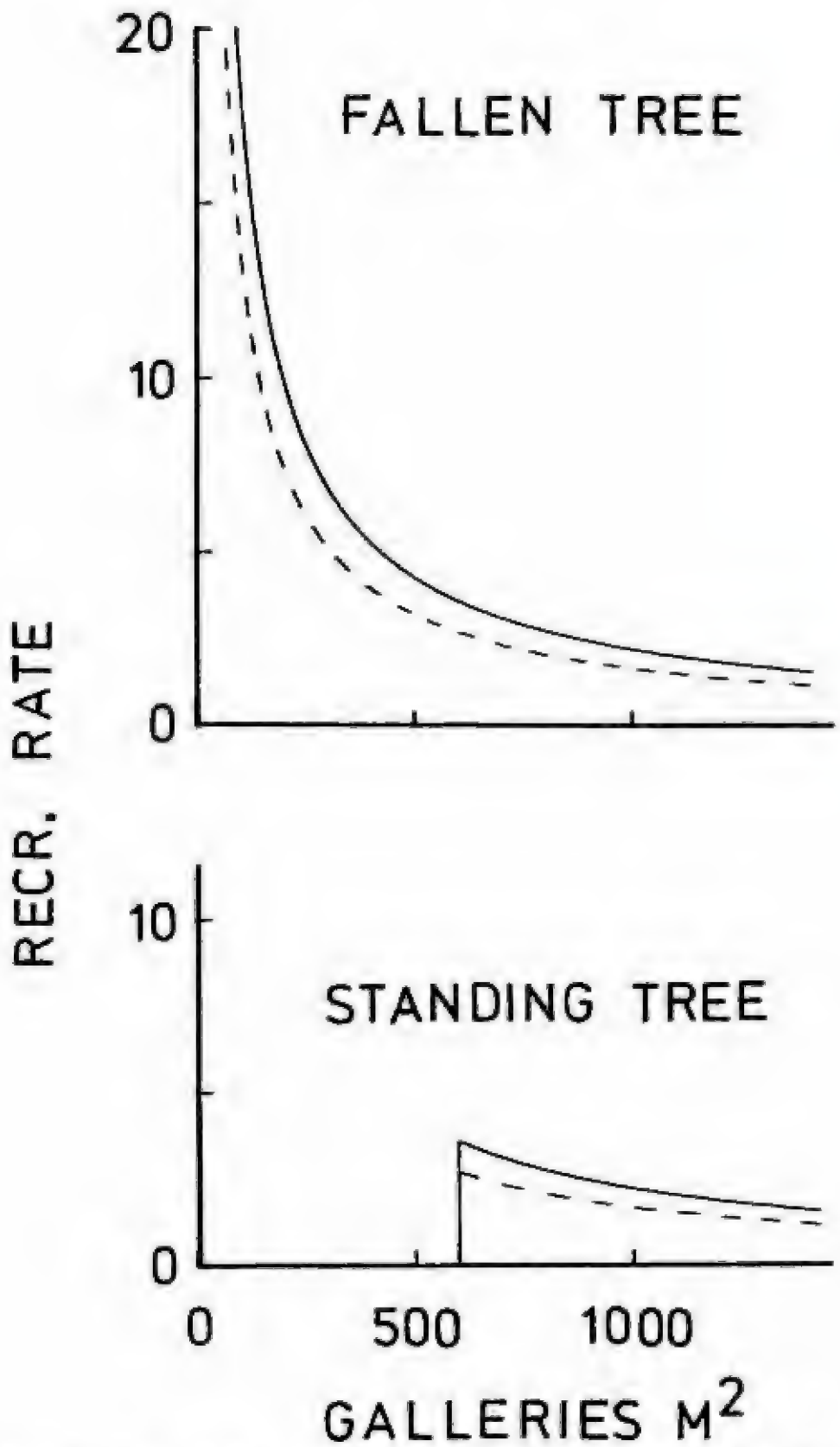

Figure 9

A model of recruitment rates (adult female offspring/female) of *I. typographus* in fallen and standing trees as a function of parent density. Solid curves show recruitment rates without mortality due to enemies (based mainly on data from Thalenhorst 1958). Broken lines exemplify hypothetical effects of enemies. The arrow indicates the approximate threshold density needed to kill a healthy, standing tree (modified after Olofsson, Forsse, Lindelöw, Regnander and Schroeder, unpublished).

the severe intraspecific competition always present in these situations (Fig 9), this evidently causes a population decline in the local patch after some years. This is illustrated by data compiled from a study of Lekander (1972) (Fig 10). During successive years in an outbreak area the replacement rate ***within*** trees decreases

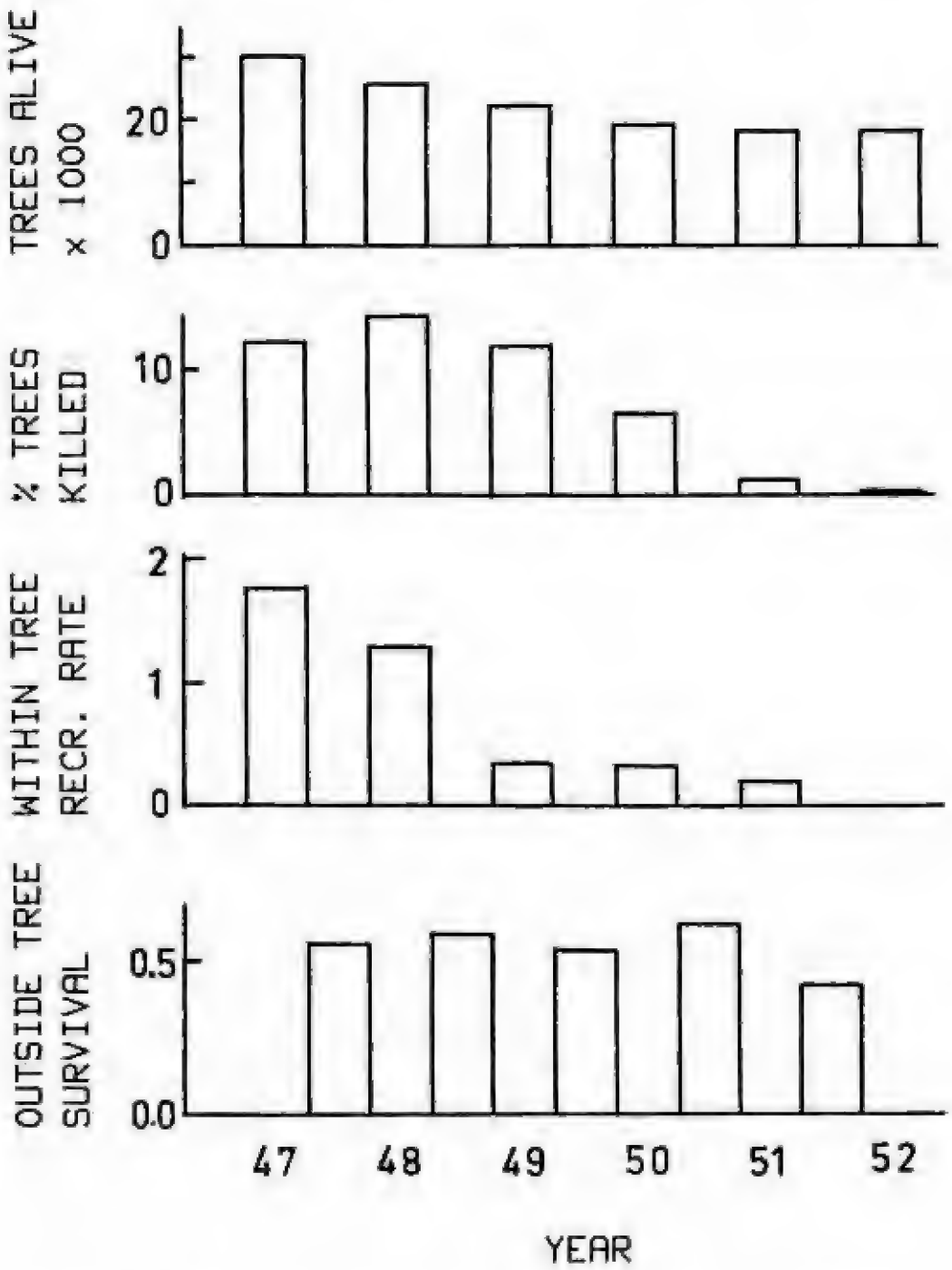

Figure 10

Changes in resource base (spruce trees with a larger diameter than 20 cm), percent of resources used by beetles, within-tree population growth of beetles and winter plus migration survival of beetles during an outbreak of *I. typographus* in central Sweden, 1947–1952 (data from Lekander 1972).

successively (probably due to the effects of enemies), while survival during the rest of the year, when the beetles are outside trees and hibernate and migrate, remains unchanged. (If, for example, tree resistance increased from year to year, this would most likely have affected "outside tree survival" by increased mortality during attack attempts.) As an outbreak proceeds it thus becomes more and more favorable to migrate farther and search for fallen trees. These are often situated far away, and thus the migrant leaves competitors and enemies behind.

In the case of *I. typographus* the environmental template is the result of complex interactions between the host plant, the herbivore and its enemy guild. Judging from flight times and field observation, the processes involved probably have a spatial scale of tens of kilometers. Furthermore, a temporal scale of several years

has to be considered to appreciate the interactions with the natural enemies. In *I. typographus* migration as an adaptation has to be evaluated against a very large and complex "template."

MIGRATION AND POPULATION DYNAMICS

In most ecology textbooks, population dynamics is viewed in the perspective of one (or a few) localities. In this "locality perspective," population change is brought about by four processes: births, deaths, emigration and immigration. In an alternative perspective a cohort of individuals and their descendants form the population irrespective of where they are (cf. Taylor and Taylor 1977, 1983). If this latter perspective is adopted, emigration and immigration fuse into one process, migration, which affects the distribution of the population. In this view migration is not analogous to births and deaths but a process that affects birth and death schedules.

There are other characteristics as well that make migration a process quite different from birth and death. Migration is usually a more rapid and synchronized process than births and, in particular, deaths. A local population of spruce bark beetles in a small forest area, for example, may grow from zero to several thousands per tree in a matter of hours.

Migration is a repeatable and reversible process. Insects emigrating may come back themselves, or their offspring may return. Migration is also a process with many behavioral and physiological steps. Death is usually a simple process, but migration is commonly preceded by many developmental steps when the insect may use "environmental information" for making "decisions" about migrating or not. The flight also has several steps during which different environmental cues are used. Another important aspect of migration is that it often consists of several repeated flights (as in ***H. abietis***, ***L. equestris*** and ***I. typographus***). This allows the insect to take off again after "evaluating" the place where it landed. It seems that such a trial and error process is quite efficient in many cases.

It is often taken for granted that migration involves great risk, a view that was recently challenged by Taylor and Taylor (1983). There seem to be few data quantifying the risks of migration (and in particular of comparing them with the risks of not migrating) which is understandable considering the practical difficulties in obtaining such data. But in many cases of short and medium-range migrations, I suspect that mortalities during migration are rather small. Both for ***I. typographus*** and ***L. equestris*** there is evidently a low mortality at least for short flights.

Many insects face environments that are highly variable in space and time. There is, for example, growing evidence of a large variability in the quality of host plants of herbivorous insects. Many insects also seem to have good abilities to track small changes in host plant quality, as in the planthopper ***Prokelisia marginata*** feeding on ***Spartina alternifolia*** (Denno 1983 and this volume), or to track changes in food resource abundance as in ***L. equestris***. Migration can thus be viewed as an important means of avoiding competition (Taylor and Taylor 1983).

There are, however, other environmental factors than food resources that are of importance in this context. There are, for example, many cases where migration ensures the tracking of regional or local (as in *L. equestris* fall migrations) climatic changes.

The least explored interaction seems to be that between the insect migrant and its natural enemies. This is undoubtedly a very important interaction in many cases, and migration can often be an important means of reducing the pressure from specialized enemies. This seems to be one important factor in the migrations of *I. typographus*.

The interactions between the migrant and its environment are often complex and the temporal and spatial scales of these processes are often underestimated. As knowledge of an insect population system increases, so usually does the appreciation of the magnitude of scales in time and space. In *I. typographus*, for example, population processes seem to have a spatial scale of perhaps tens of kilometers, and the temporal scale encompasses several years as densities switch from one stability domain (cf. Peterman, Clark and Holling 1979) to another, from endemic populations on fallen trees to epidemic ones on standing trees. The best example of such large-scale processes in space and time comes from the studies of the spruce budworm, *Choristoneura fumiferana*, in Canada, where movements in space are up to 200 km in one generation and where habitat changes have cycles of around 75 years (Greenbank, Schaefer and Rainey 1980; Holling 1978).

This highlights a specific and important methodological problem facing those that want to analyze migration as an evolutionary strategy. Migration results in the individual living the rest of its life in a new environment with new birth and death schedules. When studying most other types of behavior, one can evaluate the fitness of alternative behavioral patterns in the same environment and often over a relatively short period of time. But in the case of migration, those that behave (that is migrate) are normally lost within seconds. In the rare cases when their landing place is known, one has to take into account that all other kinds of selective pressures may be different for the rest of their lives and for their offspring.

ACKNOWLEDGMENTS

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ECOLOGICAL GENETICS OF WING LENGTH, FLIGHT PROPENSITY, AND EARLY FECUNDITY IN A MIGRATORY INSECT

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ABSTRACT

Replicated bidirectional selection for long and short wing length over 9 generations resulted in correlated responses in flight propensity and early fecundity in a migratory population of the milkweed bug *Oncopeltus fasciatus*. The incidence of long duration tethered flight in the long-wing lines exceeded that of unselected control lines after 3, 4 and 9 generations. Incidence of flight in short-wing lines did not consistently differ from that of controls. Cumulative egg production in the first five days of oviposition increased in the long-wing lines and decreased in the short-wing lines relative to the controls. These correlated responses to selection suggest that certain positive genetic correlations exist between wing length, early fecundity and flight propensity.

INTRODUCTION

The life history of an organism is comprised of a constellation of phenotypic traits which function together to enhance survival and reproduction (Stearns 1976). These traits include not only the patterns of development, fecundity and longevity, but also may include behaviors such as diapause and migration which permit flexibility in the face of seasonal or spatial variation in habitat quality (Dingle 1982). Specifically, migration affords the individual a choice of habitats for the production of offspring and the ability to escape a deteriorating habitat (Solbreck 1978).

Migratory behavior has attracted much attention from ecologists because of its role in colonization (Southwood 1962). For example, the best colonists should have the ability to disperse to the new habitat and the ability to persist once they arrive (Simberloff 1981). Migration is most directly related to dispersal while other life history variables such as rapid development, rapid reproduction and high fecundity are most directly related to persistence (Safriel and Ritte 1980). The phenotypic association between these traits in colonists is both predicted by theory (MacArthur and Wilson 1967) and observed for a number of species (Parsons 1983). However,

the extent to which these phenotypic associations are genetically based has received considerably less attention.

This study investigates the possibility of genetic correlations between three life history traits within a migratory population of the large milkweed bug *Oncopeltus fasciatus* Dallas (Hemiptera: Lygaeidae). These are: (1) forewing length, (2) flight propensity (as measured by tethered flight in the laboratory), and (3) early fecundity (total number of eggs laid per female during the first five days of reproduction).

Specifically, results presented here bear on three major questions. First, does phenotypic variation in these characters have a genetic component? This is a very basic question, but more often than not the existence of genetic variation is assumed rather than demonstrated. Second, is there genetic covariance between these characters which could influence their phenotypic evolution? For example, positive genetic correlations provide the potential for correlated phenotypic responses when selection acts on the additive genetic variance of any one of these characters (Falconer 1981). Negative genetic correlations among characters may constrain their phenotypic response if selection acts to change them simultaneously in the same direction (Lande 1979, 1982). Alternatively, a positive genetic correlation may also constrain the phenotypic response if selection acts in opposite directions at different stages in the organism's life cycle. The latter possibility may be especially relevant to migratory insects where selective pressures acting on larvae may differ radically from those acting on the adult. Third, are there patterns of genetic correlations which characterize colonizing populations or species (Parsons 1983)? This is the broadest of the three questions and one which I see as a long-term goal of empirical studies which address the first two (e.g., Ritte and Lavie 1977, Wu 1980, Rose and Charlesworth 1981, and below).

In this study I imposed strong directional selection for long and short wings and subsequently assayed lines for correlated responses in flight propensity and early fecundity. A correlated response to selection is a change in the mean phenotypic value of one trait which accompanies a response to selection in another trait (Falconer 1981). Correlated responses can result from the existence of additive genetic covariance between the traits due to pleiotropy or linkage disequilibrium. Thus the observation of consistent correlated responses across replicates provides strong evidence of common genetic influences among the traits.

METHODS

Field studies have provided broad outlines of the natural history of *Oncopeltus fasciatus* (e.g., Ralph 1977, Dingle 1981). The geographic distribution of this species spans much of Central and North America, extending as far north as southern Canada. Severe winters in Iowa prevent this species from overwintering locally. Consequently, Iowa populations consist of seasonal migrants which re-invade each summer from southern overwintering sites. Adult descendents of Iowa colonists eclose in late August through October. Decreasing daylengths and lower temperatures induce reproductive diapause, and these newly-eclosed adults emigrate, presumably to return

south.

Adult *O. fasciatus* were collected at five field sites in Johnson County, Iowa, in September 1981 to establish the laboratory population. Offspring of field-collected adults were reared at 27°C under a photoperiod regimen of 14 hr light: 10 hr dark (LD 14:10) with an abundant supply of milkweed seeds (*Asclepias syriaca*) and water. At eclosion, adults were outbred to exclude full-sib matings and maintained as male-female pairs in separate petri dishes with seeds, water, and cotton for oviposition. Pairs were randomly assigned to one of two replicates, and their offspring became the base population, generation 0 (gen. 0) of the selection experiment.

The selection experiment consisted of three lines within each replicate: a control line in which parents of each generation were chosen at random, a long line in which males and females with the longest wings in each family were selected as parents, and a short line in which males and females with the shortest forewings in each family were selected as parents. This "within-family" design was used to reduce the influence of cross-family environmental effects and to minimize the effects of inbreeding (Falconer 1981). Details of the design and results of the selection experiment will be presented elsewhere (Palmer, in preparation).

Laboratory tethered flight assays were conducted on bugs derived from generations 3, 4 and 9 of the selection experiment to detect correlated responses in flight propensity. Approximately 20 eggs from each of 10 families chosen at random within each line were reared as full-sib families at 23°C and either LD 10:14 (gen. 3) or LD 14:10 (gen. 4 and 9). The assays of generation 3 were designed as a pilot study, and only lines from the first replicate were sampled. All lines in both replicates were sampled in generations 4 and 9. In the pilot study and the first replicate of generation 4 the rearing containers were partially enclosed with plastic wrap during the first two instars until nymphs were too large to escape through the mesh lid. In the second replicate of generation 4 and both replicates of generation 9, extra-fine gauge mosquito netting was used in place of plastic wrap.

Flight propensity was assayed using tethered flight techniques similar to those described by Dingle, Blakely and Miller (1980). Bugs were attached by the pronotum to an applicator stick with nontoxic glue. Tethered bugs were suspended from a rack into a light breeze generated by a fan placed 2 m away. Adult bugs were maintained in groups of 3 to 5 full-sibs of the same sex, and flight tested at 8, 10 and 12 days post-eclosion (gen. 3 and 4) or at 8, 10 and 14 days post-eclosion (gen. 9). Each flight test consisted of five successive flights. The durations of these flights were summed to give the total duration of flight for a given bug on that day. The longest of the three daily flight totals for each bug was used to compare flight propensity between lines. Ambient temperatures during flight tests were maintained between 26.5°C and 27.5°C. Bugs were permitted to acclimate to this temperature for 30 min prior to testing and were returned between tests to the environmental regimen under which they were reared. Following their final test, bugs of generations 4 and 9 were measured for wing length under a dissecting microscope.

Early fecundity was measured as the cumulative number of eggs produced per female in the first five days after the onset of oviposition. (Thus this variable was measured independently of the adult age at which oviposition began.) Early fecundity was measured among the parents of each generation in all lines of the selection experiment and among random samples of adults within all lines in generation 7. Early fecundity was not measured among the bugs reared at 23°C for the flight experiments.

RESULTS

Divergence in Wing Length

Bidirectional selection for wing length at 27°C produced substantial divergence from unselected control lines in both replicates and both sexes (Palmer, in preparation). In nine generations of selection, mean wing length in the long lines diverged by approximately 4 standard deviations above that of the controls, while mean wing length in short lines diverged by approximately 3 standard deviations below that of controls (Table 1). Mean wing length in both control lines fluctuated within one standard deviation of that of the base population (gen. 0) over the nine generations (Palmer, in preparation).

Phenotypic differences between lines were maintained when bugs were reared at a lower temperature (23°C) for the tethered flight assay (Fig 1). Within generations, sexes, and replicates, mean wing length in selected lines differed significantly from that of their respective controls (One-way ANOVA, all comparisons $p < 0.001$ at 23°C).

Correlated Response in Flight Propensity

Flight test data are summarized as the proportion of bugs within a line for which the longest daily tethered flight exceeded 30 min in duration (Fig 2) (this is the operational criterion developed in previous studies to detect propensity for migratory flight, e.g., Dingle et al. 1980). Inspection of data for all lines over all generations revealed a striking difference in flight behavior among all lines of the pilot study (gen. 3), and replicate 1 of generation 4 compared to that of all lines in subsequent assays (Fig 2). Among the former, incidence of long duration flight in all lines (less than 12%) was much lower than previously reported results for Iowa populations (about 25−30%, Rankin 1974, Dingle et al. 1980). Major cross-generational differences common to selected lines *and* control lines are interpreted as resulting from environmental differences between generations rather than genetic differences within lines (Falconer 1981). The modification in rearing procedure between the first and second replicates of generation 4 (see Methods) may have contributed to such environmental differences, but the exact causes remain unknown. However, despite low incidences of flight in all lines of generation 3 and replicate 1 of generation 4, the qualitative trends were consistent and provided the first suggestion that flight

Table 1
Divergence in mean forewing length after nine generations of bidirectional selection in *Oncopeltus fasciatus*.

Generation	Line	Replicate	Female wing length (mm)	Male wing length (mm)
			$\bar{x} \pm$ s.d.(n)	$\bar{x} \pm$ s.d.(n)
0	"Base"	1	12.16 ± 0.48 (278)	11.01 ± 0.43 (303)
0	"Base"	2	12.21 ± 0.41 (377)	11.09 ± 0.48 (364)
9	Control	1	12.20 ± 0.37 (276)	10.99 ± 0.35 (279)
9	Control	2	12.13 ± 0.44 (242)	10.93 ± 0.37 (211)
9	Long	1	14.05 ± 0.41 (242)	12.69 ± 0.37 (234)
9	Long	2	14.17 ± 0.36 (226)	12.82 ± 0.30 (235)
9	Short	1	10.84 ± 0.53 (227)	9.85 ± 0.51 (242)
9	Short	2	11.10 ± 0.42 (216)	10.07 ± 0.40 (230)

propensity was enhanced in long-wing lines and depressed in short-wing lines relative to unselected controls (Fig 2).

Subsequent rearing methods resulted in incidences of flight among controls comparable to those of previous studies of Iowa populations. In replicate 2 of generation 4 and both replicates of generation 9, incidence of long duration flight significantly increased in the long-wing lines relative to unselected controls (Fig 2). Incidence of flight in short-wing lines did not significantly differ from that of controls. The correlated response in propensity for long duration flights among bugs selected for long wings is interpreted as evidence for common genetic influences between these two phenotypic characters. A symmetrical correlated response (decreased flight propensity) in the short-wing lines is not statistically supported by these data, although qualitatively the trend was apparent in four of the five comparisons.

Correlated Response in Early Fecundity

Early fecundity data were recorded for all females which founded each generation, in all lines. Thus these data provided a continuous record of early fecundity among the selected extreme phenotypes and unselected controls for nine generations (Fig 3). Differences in early fecundity between the female founders of the selected lines compared to founders of control lines in the base population (gen. 0) reflect a strong positive phenotypic association between wing length and early fecundity. In subsequent generations, early fecundity progressively increased among long-winged parents and decreased among short-winged parents, relative to the controls, while the control lines showed no consistent deviations from early fecundity

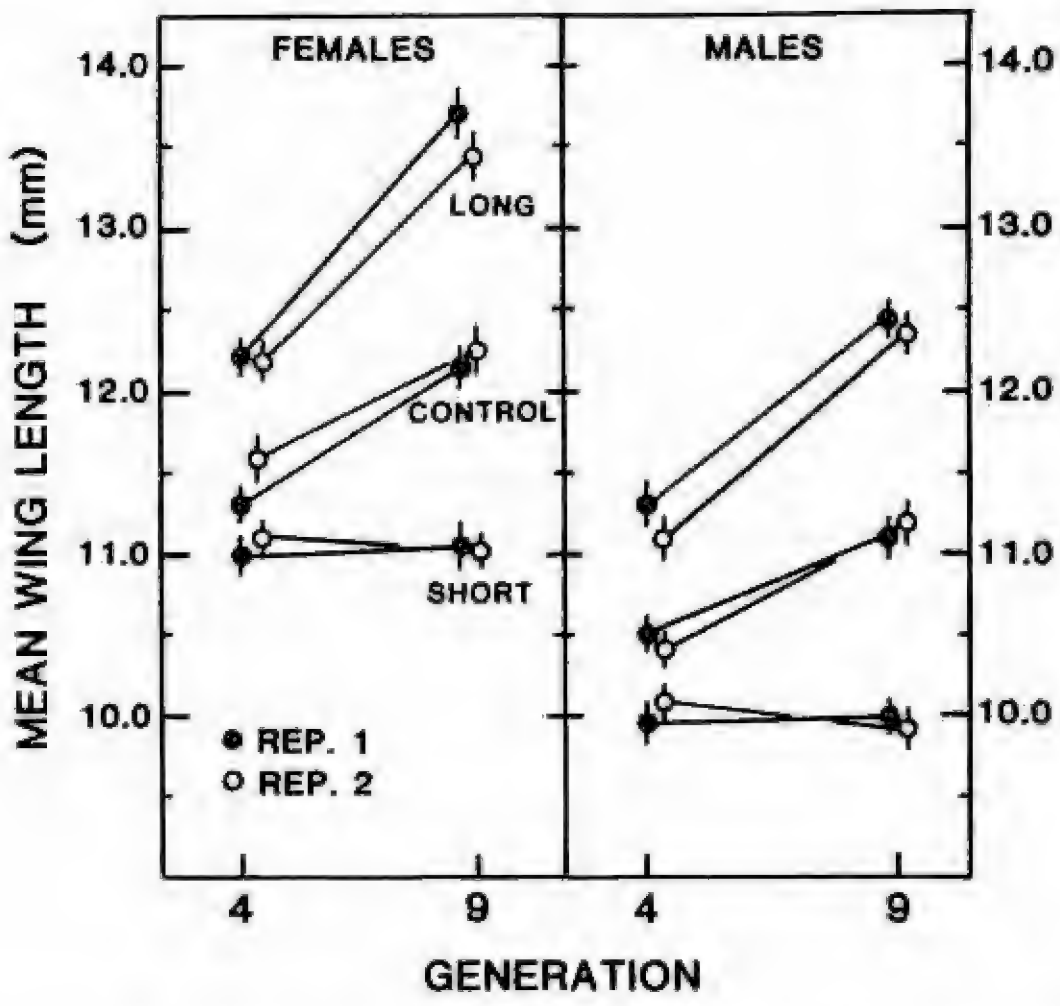

Figure 1
Differences in wing length among selected and control lines when reared at 23°C for tethered flight assays. Points indicate mean forewing length ± s.e. Sample sizes for each point range from 35–63.

of the base population (Fig 3). While these data suggest the possibility of a correlated response in early fecundity, they provide only circumstantial evidence since the behavior of extreme phenotypes within lines may not necessarily resemble that of individuals chosen at random within lines.

Correlated responses in early fecundity were investigated directly among bugs chosen at random within lines in generation 7 of the selection experiment. Results indicate that the pattern of divergence in fecundity of selected lines relative to controls was qualitatively similar to that seen among extreme phenotypes and was highly significant (Fig 4). In both replicates, early fecundity of control lines did not differ significantly from that of the base population. In long-wing lines, early fecundity increased by about 20% relative to the controls, and in short-wing lines it decreased by about 20% relative to the controls. These results are interpreted as strong evidence for common genetic influences between forewing length and early fecundity in Iowa *O. fasciatus*.

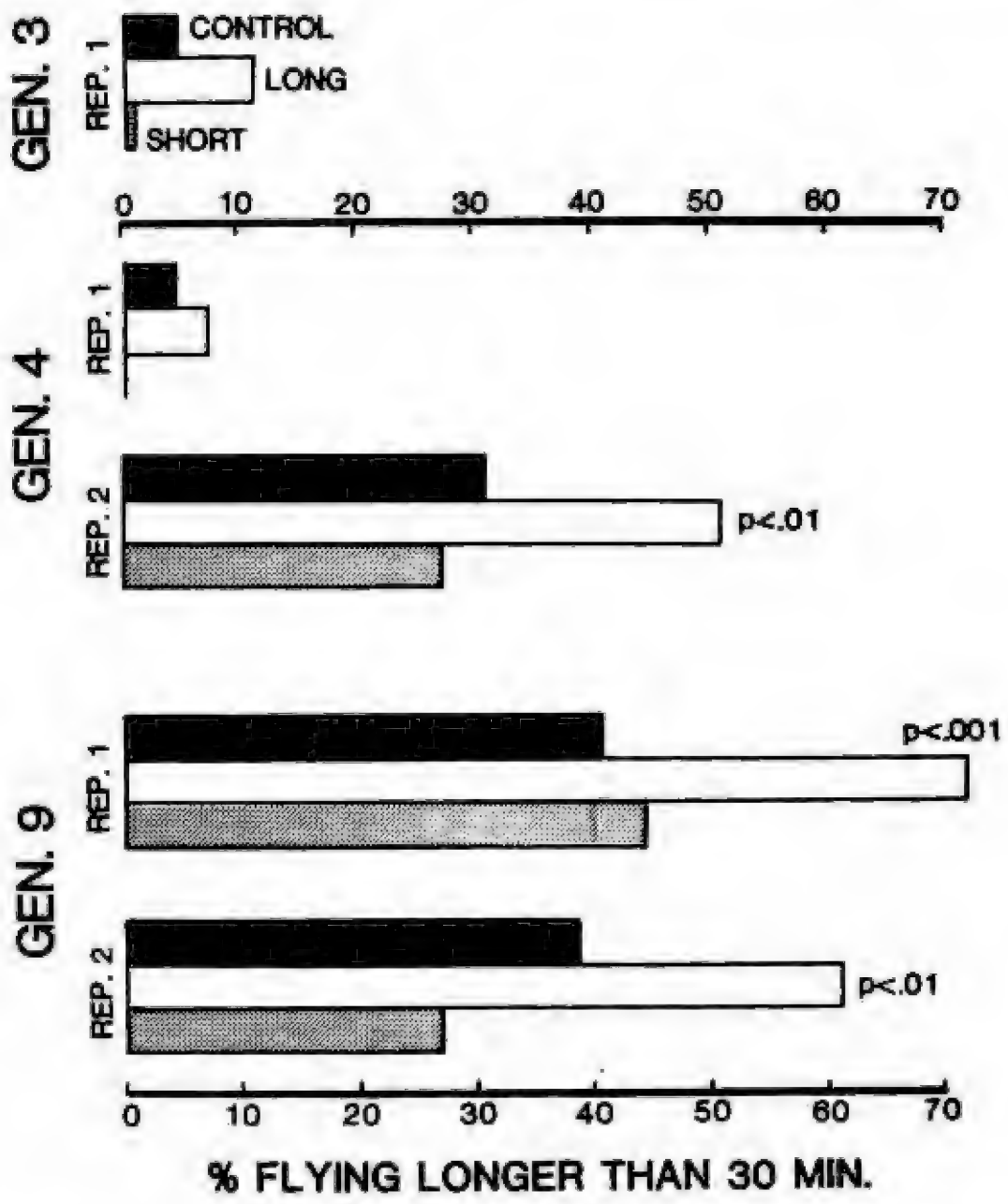

Figure 2

Correlated response in flight propensity. Percent of bugs which flew for longer than 30 min on any day of the three-day assay (see Methods) are presented for each line of the three generations assayed. Sample sizes within each cell (line) range from 70−120 individuals. Chi-square values were evaluated for pairwise, one-tailed comparisons between each selected line vs. their respective control. Comparisons which showed significant differences at the 0.05 level or less are indicated.

DISCUSSION

Artificial selection on wing length within a migratory population of the milkweed bug *Oncopeltus fasciatus* resulted in major phenotypic and genetic differences between lines for that trait. This direct response to selection was accompanied by correlated responses in flight propensity and early fecundity. These results provide strong evidence for the existence of positive additive genetic covariance between wing length and flight propensity, and wing length and early fecundity. The genetic association between the latter traits supports predictions previously derived from genetic analysis of an Iowa population (Hegmann and Dingle 1982). Results of this study do not, however, permit any inferences regarding the existence of genetic covariance between flight propensity and early fecundity. Investigation of this possibility is in progress (Palmer, in preparation).

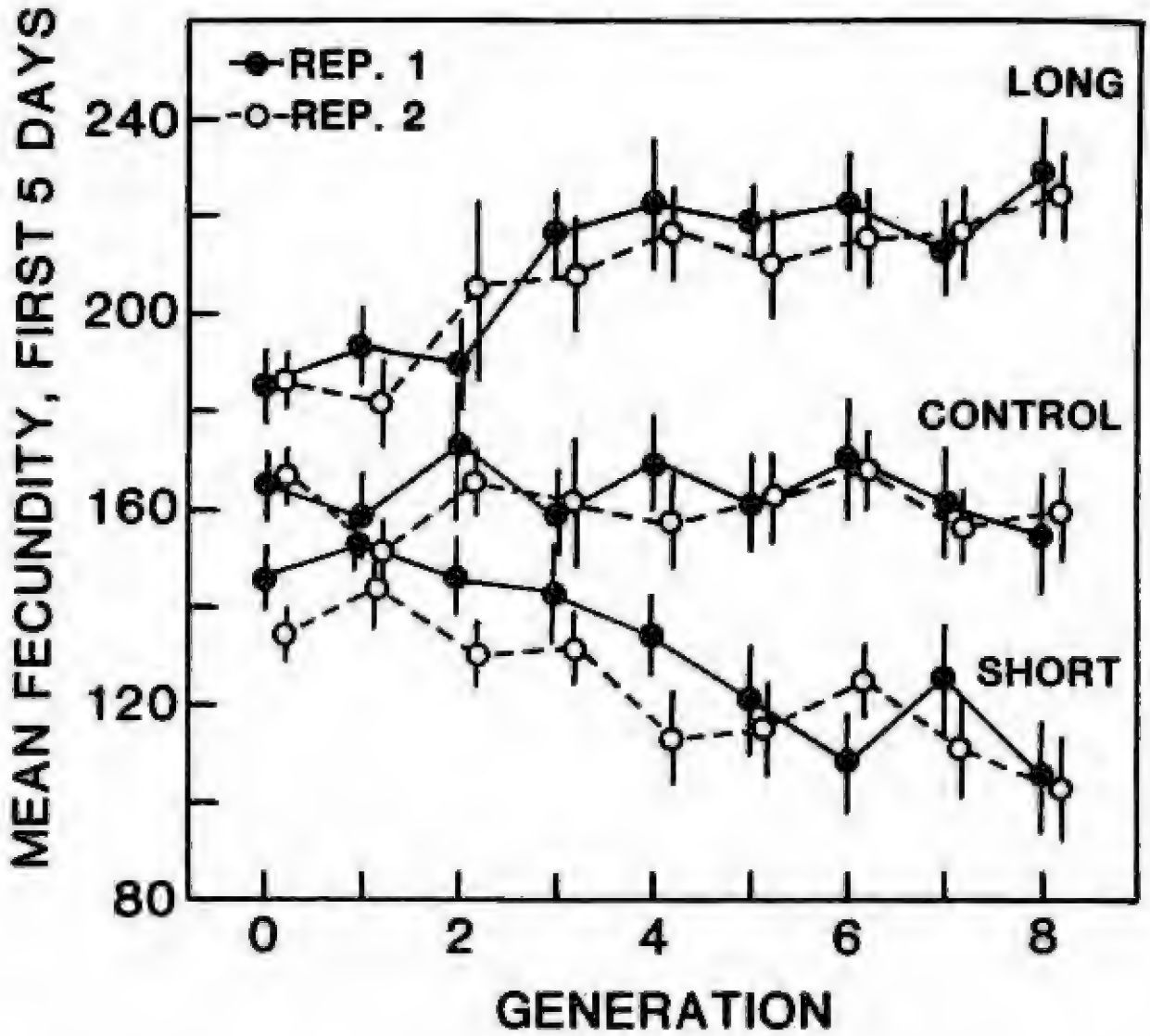

Figure 3

Divergence in early fecundity among selected parents. Points indicate mean cumulative egg production during the first five days of oviposition for all females within each line, within each generation. Vertical bars indicate ± s.e. Sample sizes for each point range from 12–19.

For *O. fasciatus*, as for many other species, migratory behavior may be adaptive if it enhances reproduction, or survival, or both, under selective regimes imposed by temporally or spatially ephemeral habitats. This hypothesis is supported by numerous ecological studies (Southwood 1962, Dingle 1972, Baker 1978). An overriding assumption, however, is that the phenotypic components of migratory behavior have a genetic basis such that they could respond to selection, and respond in the hypothesized direction. Central to this issue is a knowledge of the genetic covariance among phenotypic traits (Lande 1979, 1982; Dingle 1983). For Iowa *O. fasciatus*, results of this study provide some tentative insight to these questions.

First, do phenotypic differences observed within a single character possess sufficient additive genetic variation such that the character could respond to selection? Direct and correlated responses to artificial selection in wing length, flight propensity and early fecundity provide strong evidence that the answer is yes for this population.

Second, is there genetic covariance between characters which could influence their phenotypic response to selection? Migratory behavior is a complex phenotypic character of which flight propensity is only one component. Results of this study suggest that migratory behavior in milkweed bugs may be enhanced not only by direct

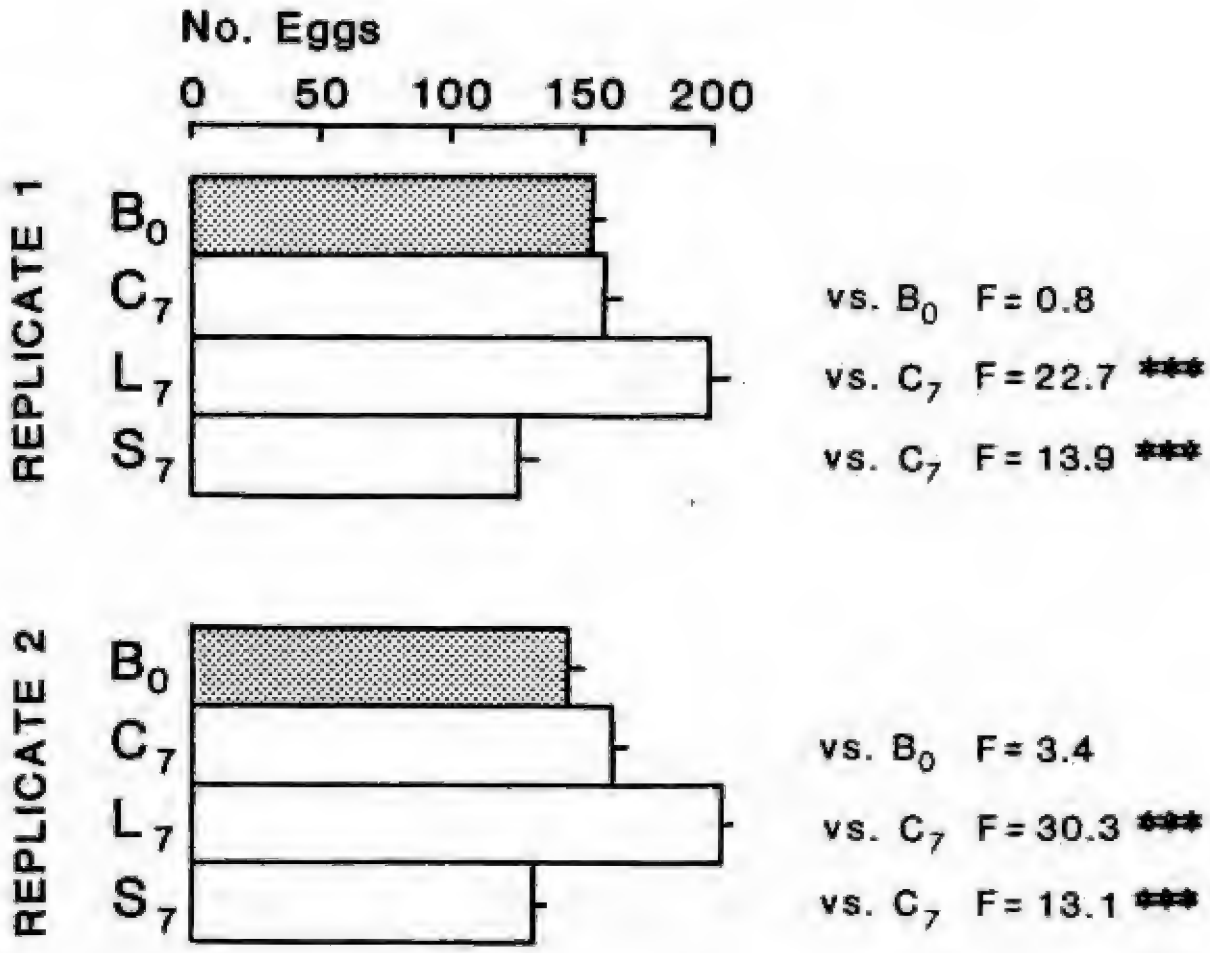

Figure 4

Correlated response in early fecundity. Mean cumulative egg production during first five days of oviposition (± s.e.) is indicated for each line of generation 7 as well as the base population (B_0) shaded bars). One-way ANOVA comparisons between control lines vs. their respective base population, and selected lines vs. their respective controls are shown; *** indicates $p < 0.001$. Sample sizes in each cell range from 49–67.

effects of selection to increase flight propensity, but also indirectly if selection simultaneously favors traits that share positive genetic covariance with flight propensity, namely, wing length and possibly early fecundity. Furthermore, these results have detected positive genetic covariance among traits that have been previously found to exhibit positive phenotypic covariance in this species (Dingle et al. 1980, Hegmann and Dingle 1982). An especially important question for organisms with complex life cycles is the extent to which genetic covariance exists between larval and adult characters. For *O. fasciatus*, if larval and adult size-related characters are positively correlated genetically, then selective pressures in the larval environment that oppose large nymphs, such as food limitation during larval development (Blakely 1981), would simultaneously oppose an increase in adult wing length and conceivably constrain the phenotypic response towards increased flight potential in adults of a migratory population. Experiments to evaluate this possibility are in progress. Artificial selection experiments, parent-offspring analyses and sib analyses are powerful tools for assessing the existence and direction (sign) of genetic variances

underlying phenotypic characters. The formidable challenge for ecologists is the identification of the relevant selective pressures at all stages of the life cycle.

Third, are there particular patterns of genetic correlations which characterize colonizing populations or species (Parsons 1983)? This is the broadest question and it must be approached empirically by comparing the genetic covariance structures of "colonizing" and "noncolonizing" populations or species. Significant insight cannot be expected to derive from just a few studies. Nevertheless, results presented here suggest that the question is tractable, and artificial selection can elucidate patterns of genetic covariance in the suite of traits associated with colonizing ability.

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WING POLYMORPHISM IN WATERSTRIDERS (GERRIDAE: HEMIPTERA): MECHANISM OF MORPH DETERMINATION AND FITNESS DIFFERENCES BETWEEN MORPHS

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ABSTRACT

Genetic and environmental factors influencing wing polymorphism in the waterstrider ***Limnoporus canaliculatus*** were investigated by rearing progeny of single pair crosses in different photoperiods. There was a strong genetic component to morph determination, but results were inconsistent with a single locus, two allele mode of inheritance under either photoperiod. Photoperiod strongly influenced morph determination, and results were consistent with observed seasonal variation of morph frequencies in natural populations. These results are at variance with previous reports of a single locus (or supergene), two allele mode of inheritance of the trait in gerrids and have implications for current models of the evolution of winglessness and dispersal.

Fitness differences between the long-winged and wingless morphs of ***L. canaliculatus*** were also investigated in the laboratory. The long-winged morph exhibited significantly higher survivorship under laboratory-simulated overwintering conditions, and the results were consistent with dramatic changes in morph frequencies during the overwintering period in natural populations. In contrast, the wingless morph exhibited a faster nymphal development rate and higher female fecundity than the long-winged morph, and results were consistent with other studies of these traits in wing polymorphic insects.

INTRODUCTION

Wing polymorphism commonly occurs in many insects, especially species of Orthoptera, Coleoptera, Homoptera and Hemiptera (Harrison 1980). The polymorphism (see Materials and Methods for definitions) consists of discrete differences in winglength with morphs exhibiting fully developed, reduced or totally absent wings. Besides differing in winglength, morphs typically differ in a number of anatomical, physiological and life history traits. Thus wing polymorphism is a syndrome of traits resulting in morphs which are adapted to reproductive/sedentary versus diapause/dispersing lifestyles (Vesäläinen 1978, Dingle 1982).

Wing polymorphism is an attractive system for investigating the evolution of dispersal in natural populations. Individuals with radically different dispersal characteristics are "packaged" into identifiable and discontinuous morphs. Thus laboratory studies of the genetic and environmental bases of dispersal characteristics and field studies of associations between dispersal ability and environmental variables are far simpler in these species than in species containing only fully winged individuals.

Waterstriders (Gerridae: Hemiptera) represent an excellent group in which to study the evolutionary dynamics of wing polymorphism. Many species are wing polymorphic, and there is considerable variation in the spatial and temporal patterns of morph frequencies among different species (Vepsäläinen 1978, Calabrese 1979). Moreover, many species are wing or wingless monomorphic, and thus intraspecific studies of wing polymorphism can be combined with interspecific studies to yield very powerful tests of particular hypotheses of dispersal. It is not surprising, therefore, that wing polymorphism has been particularly well-studied in this group (reviewed in Vepsäläinen 1978). However, despite numerous studies, the forces influencing wing polymorphism in natural populations of waterstriders still remain poorly understood.

A first step in understanding the adaptive basis of wing polymorphism in natural populations is identifying the environmental and genetic influences on morph determination (Harrison 1980). The role of various environmental variables such as photoperiod, temperature, density, etc. has been studied in a number of insects. However, we know little about the genetic component of morph determination or about potential genotype by environment interactions. Yet such information is a prerequisite for even the most basic ecological genetic studies. Moreover, the validity and conclusions of many models of the dynamics of wing polymorphism and the evolution of winglessness critically depend upon assumptions concerning the mechanisms of morph determination (Zera, Innes and Saks 1983).

There have been several attempts to determine the genetic basis of wing polymorphism in gerrids, more so than for any other group of wing polymorphic insects (reviewed in Zera et al. 1983). The most commonly held view has been that the polymorphism is controlled by a single locus with two alleles, the effect of which is modified by the environment. The allele for short wings is purported to be dominant to the allele for long wings such that long-winged individuals are recessive homozygotes. However, there are substantial problems with these studies, with respect

to both experimental design and interpretation of results (Harrison 1980, Dingle 1982, Zera et al. 1983).

A second and equally important piece of information needed to understand the adaptive basis of wing polymorphism is data on fitness differences among morphs of differing winglength. Such data provide direct evidence for trade-offs between dispersal versus reproductive ability and indicate potential mechanisms of selection. Fitness differences (often assumed) among dispersing and nondispersing morphs also form the basis of models of the evolution of dispersal (for example, see Vepsäläinen 1978). Despite considerable speculation, there are few reliable data on fitness differences between the long-winged and the short-winged or functionally equivalent (Anderson 1973) wingless morphs in gerrids (Zera 1984).

In this paper I will discuss recent studies of the mode of inheritance and fitness differences between the long-winged and wingless morphs of a model waterstrider *Limnoporous canaliculatus*. These studies represent the beginning of an in-depth study of the genetics, physiology and developmental biology of the wing polymorphic adaptive complex in this species. The specific questions dealt with here are: (1) is the genetic basis of morph determination in *L. canaliculatus* consistent with a single locus, two allele model, (2) do morphs of differing winglength differ in such fitness traits as overwintering survivorship, fecundity and development rate, and (3) are the observations of the genetic and environmental influences on morph determination and the fitness differences between morphs which have been observed in the laboratory consistent with data from natural populations.

MATERIALS AND METHODS

Definitions

Wing polymorphism may be the consequence of genetic differences between morphs (genetic polymorphism), environmental conditions under which the morphs develop (environmental polyphenism), or a combination of the two. The term polymorphism is used here with no implication as to whether morphs are genetically differentiated or are the consequence of different environmental conditions during development. The terms genetic polymorphism or environmental polyphenism are used only when it is clear that morph differentiation is a consequence of genetic or environmental variation, respectively.

Species Studied

Limnoporous canaliculatus is a semi-aquatic hemipteran which occurs on the surface of ponds or streams. The species is distributed from Maine to southern Florida and as far west as Texas (Calabrese 1979, Zera 1981). Populations of *L. canaliculatus* consist of various proportions of fully-winged (macropterous, MAC), wingless (apterous, APT) and, rarely, short-winged (micropterous, MIC) morphs (Zera 1981, Zera et al. 1983). Populations south of Massachusetts are composed almost

exclusively of wingless individuals in the summer and varying proportions of winged individuals in the fall. Fall polymorphic populations of this species exhibit dramatic spatial variation of morph frequencies (Zera et al. 1983).

Briefly, the life cycle of *L. canaliculatus* in New England is as follows (Calabrese 1979, Zera 1981). Overwintering occurs in the adult stage. In the spring (April) adults emerge, mate, lay eggs and die shortly thereafter. The resultant progeny comprise the summer, sedentary, reproductive generation. Offspring of this generation and possibly some offspring produced by mating of overwintered adults late in the spring emerge in late summer and fall (August to early October) in reproductive diapause and leave the water surface in mid- to late October. An unknown proportion of winged individuals disperse to overwintering sites. Thus, as in other gerrids (Vepsäläinen 1978), a major feature of the life-cycle of *L. canaliculatus* is an alternation of a sedentary-reproductive generation with a diapause-dispersing generation.

Crossing Experiments

Crossing experiments essentially involved rearing progeny of pair crosses under two different photoperiod regimes: (1) short-decreasing (SD; 16 light, 8 dark with the light phase decreased by 15 minutes every two days) mimicking fall conditions and (2) long-constant (LC; 16 light−8 dark) mimicking summer conditions. This was done to determine if the genetic basis of morph determination differed under various photoperiods as well as to investigate the influence of photoperiod per se on morph determination. Other environmental variables such as density, temperature and food were kept as constant as possible. Prior to genetic studies, a generation was reared in the laboratory to eliminate possible maternal effects, to obtain virgin females and to obtain a generation reared under known conditions. A key feature of the crossing experiments was the use of a "split-brood design," that is, portions of the same brood were reared under different photoperiod regimes. This design was important in eliminating intercross variation in studies of the influence of photoperiod on morph determination. Additional details of crossing experiments may be found in Zera et al. (1983).

Fitness Studies

Three components of fitness were studied in winged and wingless morphs of *L. canaliculatus*: overwintering survivorship, development rate and fecundity (Zera 1984). In the overwintering survivorship experiment, adults were collected in the field during the fall just prior to the time when gerrids leave the water surface to overwinter. They were transported to the laboratory where they were kept in an environmental chamber at 6°C for one month without food. After this time the number of dead and surviving winged and wingless morphs of each sex was recorded. Surviving individuals were used in the fecundity experiment. This was done to mimic conditions in natural populations where reproduction of winged and wingless morphs

occurs in the spring after the overwintering period. Differences in fecundity between winged and wingless females were measured by counting the number of fertile eggs produced each day or every other day by females of individual pair crosses, during a 21-day period. Development rate of winged and wingless morphs was measured as the time from egg hatch to adult emergence at 22 ± 2°C. Individuals used in development rate studies were F_1 progeny of a mass mating of field collected adults. Additional details of these experiments may be found in Zera (1984).

RESULTS AND DISCUSSION

Mechanism of Morph Determination

Results of representative crosses are given in Table 1. These data clearly demonstrate a strong genetic component in morph determination. Under each photoperiod, the frequency of long-winged (MAC) progeny from each MAC × MAC cross was greater than that from virtually all MAC × APT (wingless) or APT × APT crosses. In general, the frequency of MAC progeny from each MAC × APT cross was greater than that from the APT × APT crosses. More importantly, the production of both MAC and APT progeny in nearly all MAC × MAC and APT × APT crosses, in each photoperiod, clearly indicates that the genetic basis of morph determination is more complex for this species than the widely held single locus, two allele model. Only 3 of 858 individuals were short-winged (MIC), and they are not dealt with here (see Zera et al. 1983, for details).

In eight of nine crosses, a higher proportion of MAC progeny was produced in the short-decreasing versus the long-constant photoperiod, thus demonstrating a strong effect of photoperiod on morph determination (Table 1). These results are similar to the influence of photoperiod on morph determination in many other insects (Harrison 1980). Results were also consistent with morph frequency data from natural populations. That is, a higher proportion of MAC progeny was produced under photoperiodic conditions similar to fall conditions during which winged morphs are produced in natural populations of *L. canaliculatus* (Zera et al. 1983).

Morph determination was also sex influenced, and the influence of sex was photoperiod dependent. A higher proportion of winged females than winged males was produced in the short-decreasing but not in the long-constant photoperiod (data not shown; see Zera et al. 1983). This result is also consistent with field data, where a significantly higher frequency of winged females than winged males was found in fall populations of *L. canaliculatus* (Zera 1984). This suggests that in the field dispersal rates may differ between the sexes.

These preliminary results indicate a complex interaction among genetic and environmental variables in morph determination. The degree of complexity of the genetic component of morph determination cannot yet be ascertained. The trait could be controlled by genetic mechanisms ranging from a large number of polygenes to a major gene with a few modifiers. Additional crossing experiments as well as studies of the physiological basis of morph determination which are in progress will provide

Table 1

Results of single pair crosses of *Limnoporus canaliculatus* with progeny reared under a single or divided between each of two photoperiods (data from Zera et al. 1983). MAC = Macropterous, long-winged; APT = Apterous, wingless. Only a few (0.5%) short-winged morphs were produced, and they are not considered here.

Parental Phenotype	Cross Name	Photoperiod Treatment: Long-Constant Photoperiod, Number (proportion) of Progeny		Photoperiod Treatment: Short-Decreasing Photoperiod, Number (proportion) of Progeny	
		MAC	APT	MAC	APT
MAC × MAC	A	14 (0.88)	2	13 (0.93)	1
	B	26 (0.52)	24	50 (0.93)	4
	E	8 (0.73)	3	21 (0.78)	6
	D	24 (0.80)	6	No Data	
	F	12 (0.38)	20	No Data	
APT × APT	I	0 (0.00)	21	5 (0.25)	15
	J	1 (0.02)	42	4 (0.57)	15
	L	1 (0.07)	14	3 (0.30)	7
	P	6 (0.25)	18	1 (0.08)	11
	M	4 (0.07)	56	No Data	
	O	0 (0.00)	29	No Data	
APT male × MAC female	G	15 (0.54)	13	No Data	
MAC male × APT female	H	5 (0.05)	87	16 (0.41)	23
	Q	3 (0.08)	33	13 (0.34)	25

crucial information on this point.

Unfortunately, since there are no reliable genetic data on morph determination in other gerrids, it is not possible to generalize from the results of this study. Limited studies of other non-coleopteran insects have also demonstrated a complex genetic component of morph determination (Harrison 1980). Only in the weevil ***Sitona hespidula*** (Jackson 1982) is there unambiguous evidence that morph determination is under control of a single gene or two forms of a supergene. Limited evidence reported by Lindroth (1946) also suggests that morph determination in the coleopteran ***Pterostichus anthracinus*** may be under control of a single gene with two alleles, thus indicating that beetles may differ from other insects in the genetic basis of morph determination.

The results for ***L. canaliculatus*** have implications for models of the dynamics of wing polymorphism in natural populations. Computer simulations of the dynamics of dispersal polymorphisms by Roff (1975) have demonstrated that employing single gene versus multigenic modes of morph determination strongly influences the outcome of these simulations. Results of this study indicate that biologically meaningful data for gerrids and for most other insects necessitates the incorporation of multigenic control of morph determination in such simulations.

Many workers have postulated heterozygote superiority as an important force in the maintenance of wing polymorphism in gerrids (Brinkhurst 1959). Besides the absence of any data on the superiority of the purported heterozygous short-winged morph, heterozygote superiority alone is not a sufficient condition for the maintenance of a polymorphism more complex than a single locus with two alleles (Crow and Kimura 1970). Other models that are based on the assumption that morph determination is controlled by a single locus with two alleles, such as the evolution of dominance of the allele for short wings (Vepsäläinen 1978), also seem inappropriate.

As pointed out by Harrison (1980), in all single gene models of wing polymorphism, where the allele for short wings (functionally equivalent to winglessness, Anderson 1973) is dominant to the allele for long wings, the only morph that is capable of dispersal is the homozygous recessive, long-winged morph. Thus if premigration mating does not occur, which is probably the case for gerrids, the spread of the allele for short wings into new habitats must occur by mutation or by dispersal mechanisms other than flight. However, once the mode of inheritance of wing polymorphism is shown to differ from the single locus, two allele model, the introduction of the allele for winglessness into new habitats is no longer problematical. In this study, wingless progeny were produced in all crosses in which both parents were long-winged. Consequently, alleles for winglessness may be transmitted into newly colonized habitats via normal dispersal by flight, even if females are not inseminated prior to dispersal.

Fitness Differences Between Morphs

The long-winged and wingless morphs differed significantly in each of the three fitness traits investigated. For both sexes, the long-winged morph exhibited greater survivorship under laboratory-simulated overwintering conditions (Table 2). The results are consistent with an increase in the frequency of the long-winged morph during the overwintering period in natural populations of ***L. canaliculatus*** (Zera 1984). On the other hand the wingless morph exhibited a substantially faster rate of nymphal development than the winged morph (Table 3). Wingless females also exhibited significantly greater fecundity than long-winged females (Table 4). Wingless females laid a greater number of eggs than long-winged females on eight of nine days on which egglaying was recorded, and the difference was greatest in the early stages of egglaying.

Table 2

Differential survivorship of the long-winged and wingless morphs of *L. canaliculatus* under laboratory-simulated overwintering conditions. Individuals were kept for one month without food at 6°C (data from Zera 1984).

		Condition	
SEX	MORPH TYPE	ALIVE	DEAD
Males	MAC	27	1
	APT	48	12
Females	MAC	51	4
	APT	51	15

RESULTS OF THREE-WAY G-TESTS USING LOG-LINEAR MODELS[1]

Independence of mortality and morph type for each sex: $G = 10.80$, 1 df, $p < 0.005$

Mortality × Sex × Morph Interaction: $G = 0.25$, 1 df, $p > 0.1$, n.s.

[1] Sokal and Rohlf (1981)

Differences in overwintering survivorship has been one of the few fitness differences demonstrated between gerrid morphs. In laboratory studies Ekblom (1941) reported a greater overwintering survivorship of the wingless morph relative to the short-winged morph in *Gerris asper*, while Vepsäläinen (1974) reported that the long-winged morph exhibited greater overwintering survivorship than the short-winged morph in *G. lacustris*. Thus there is at present no consistent difference in overwintering survivorship between the two functional morph types. Differences in survivorship between morphs under stress have been reported for other wing polymorphic or flight muscle polymorphic insects (reviewed in Harrison 1980, Dingle 1982), and again, no consistent differences among morphs were reported.

Several studies have compared development rate between morphs of differing winglength in gerrids (see Zera 1984). However, in these studies, either sample sizes were not reported, statistical testing of results was not performed, or no significant differences were observed in preliminary experiments with small sample sizes. The faster development rate of the wingless morph relative to the long-winged morph observed in this study is consistent with the results of many other studies in a variety of other insects (Harrison 1980, Dingle 1982) and appears to be a general characteristic of a particular functional morph.

Table 3

Development time (days) from egg hatch to adult eclosion for the long-winged (MAC) and wingless (APT) morphs of *Limnoporus canaliculatus*. Developmental time was measured at 22°C. See Methods for additional details.

MEAN DEVELOPMENT TIME (DAYS)				
	Males		Females	
	Winged	Wingless	Winged	Wingless
Mean	25.77	25.05	26.33	24.46
S.E.M.	0.14	0.22	0.13	0.29
Sample Size	88	37	76	24

RESULTS OF TWO-WAY ANOVA[1]			
Source of Variation	df	MS	F
Morph	1	0.657628	40.74[a]
Sex	1	0.002067	0.13, n.s.
Interation	1	0.119576	7.41[b]
Error	221	0.016142	

[1]Two-way analysis of variance was performed on squre-root transformed development rate data.

[a]$p < 0.001$

[b]$p < 0.01$

Differences in fecundity between morphs of *L. canaliculatus* observed in this study are also consistent with data for non-gerrids (Harrison 1980, Dingle 1982), and higher fecundity appears to be a general characteristic of the nondispersing morph. A variety of investigators have searched for, but in general have failed to find, fecundity differences between morphs in other gerrids (Zera 1984). However, as in the developmental rate studies, the sample sizes have been very small. Thus these studies do not constitute adequate tests of realistic fitness differences which may be present in these species. Anderson (1973) has demonstrated that in the field, short-winged *G. lacustris* attained reproductive maturity faster than the fully winged morph.

Each of the morph-associated traits studied in *L. canaliculatus* was measured under only one set of conditions, and the generality of these results is therefore unknown. However, the correspondence between development rate and fertility differences between morphs of *L. canaliculatus* with data from a variety of other studies (Harrison 1980, Dingle 1982), makes it likely that these differences are manifest under a variety of conditions both in the laboratory, and in natural populations. The correspondence between morph-dependent differences in survivorship during overwintering conditions in the laboratory, and morph frequency changes in natural populations suggests that differential overwintering ability may be

Table 4

Total number of eggs laid by winged and wingless females of *Limnoporus canaliculatus* on successive one or two-day intervals. The experiment consisted of 30 winged and 30 wingless females. Data are from Zera (1984).

Date of egg collection[1]	Total number eggs laid		Percent increase wingless/winged
	Winged females	Wingless females	
1–8	0	0	0.00
9	9	49	444.44
10	41	45	9.75
11	111	174	56.75
12	36	152	322.22
13	156	102	−34.61
Subtotal, days 9–13	353	522	47.87
15	398	425	6.78
17	439	567	29.16
19	311	390	25.40
21	429	470	9.55
Subtotal, days 15–21	1577	1852	17.44
Total	1930	2374	23.01

[1]Number of days after mating pairs were initiated. $\chi^2 = 5.44$, $p < 0.025$: sign test of number of days on which wingless females laid more eggs than winged females, one-tailed test with the a priori expectation that wingless females would lay more eggs than winged females. This expectation is based on the higher fecundity of short-winged versus long-winged morphs in a wide variety of insects (see Harrison 1980, Dingle 1980). $\chi^2 = 8.81$; $p < 0.005$: χ^2 test of the proportion of eggs laid by winged and wingless females on days 9–13 vs 15–21.

an important determinant of morph frequencies in natural populations.

For several reasons, the fecundity differences between morphs observed in this study may be magnified in the field. As mentioned above, the higher fecundity of the wingless versus the long-winged morph was particularly pronounced in the early stages of the egglaying period. The increased difference early in reproduction may compound the overall fecundity difference because of the increased probability of survivorship of early clutches due to cannibalism of older progeny on younger progeny. Cannibalism of older nymphs on younger nymphs is known to occur

commonly in both laboratory and field populations of many gerrids (see references in Jarvinen and Vepsäläinen 1976). In addition, fecundity differences were measured in winged females which had not flown. Roff (1977) demonstrated that flight significantly reduces egg production in *Drosophila melanogaster* (however, see Slansky 1980). It is therefore possible that fertility differences between morphs are even greater than those demonstrated in this study, especially since dispersal flights appear to be more common in *Limnoporous* than in *Gerris* species (John Spence, personal communication).

Since the overwintering survivorship and female fertility experiments were performed on field-collected individuals, it is not known to what degree these differences represent differences between environmentally polyphenic versus genetically polymorphic forms. The resolution of this important question must await the results of future studies. On the other hand, since developmental rate studies were performed on individuals reared in the laboratory, these differences must be due to genetic differences or maternal effects.

CONCLUSIONS

Results of this study provide some preliminary answers to the questions concerning the adaptive basis of wing polymorphism stated above. Obviously, additional experiments both on the mechanism of morph determination and on the fitness differences between the winged and wingless morphs are needed before these questions will be satisfactorily answered. In addition there are other important questions concerning wing polymorphism for which there is no information. For example, the biochemical and physiological bases of the fitness differences between morphs of differing winglength remain totally unknown. Nor is there any information on the mechanisms underlying the coordination of the traits comprising the wing polymorphic adaptive complex.

Viewed from a different perspective, wing polymorphism is a developmental polymorphism. Individuals are genetically programmed and/or are directed by environmental variables to proceed along different developmental pathways, both resulting in morphs of differing winglength. As pointed out by Harrison (1980), a sufficient understanding of the adaptive basis of wing polymorphism requires unraveling these developmental mechanisms and determining how variation in development is influenced by ecological factors. This necessitates a multi-disciplinary approach involving ecology, physiology and developmental biology. The information on wing polymorphism in *L. canaliculatus* provides a foundation for such studies which are currently in progress.

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THE ADAPTIVE SIGNIFICANCE AND CONTROL OF MIGRATORY BEHAVIOR IN THE GRASSHOPPER *MELANOPLUS SANGUINIPES*

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ABSTRACT

Little attention has been given to the degree of variability in the migratory behavior of grasshoppers and locusts. Work on ***Melanoplus sanguinipes*** indicates that there is considerable temporal and geographic variability in migration in at least this species. Despite the emphasis given to density as a factor in locust behavior and physiology, the role of density as a causal factor in migration of locusts is not entirely understood. In addition, there has been no attempt to address the question of the extent to which migratory behavior in locusts has a genetic component. Recent work on ***M. sanguinipes*** suggests that, although environmental factors may modulate the degree of migratory behavior, genotype has the greatest influence. Development of mass swarms of this species may be the result of relatively rapid selection imposed over a small number of generations.

INTRODUCTION

Many species of grasshoppers and locusts are quite spectacular and economically important migrants. At least two African species, ***Locusta migratoria*** and ***Schistocerca gregaria*** make annual seasonal movements between summer and winter breeding areas. However, migration in most acridids, though seasonal, does not involve predictable return by a subsequent generation. Species with such non-circuit patterns of movement might be expected to display variability in the destinations and the distances traveled from year to year and from one geographic location to another. To the extent that the proportion of migrant individuals also differs between populations or over time, the question of the relative contribution of environmental and genetic factors to variation in migratory behavior must be addressed. The determination of whether an individual becomes a migrant could theoretically depend strictly on genotype or on environmental conditions experienced during nymphal development (or by the mother) or on the interaction of genetic and environmental factors.

These alternatives have different implications for the development of mass migrations in a population, the ability of a species to invade new habitats, the maintenance of migratory behavior in the face of counteracting selection pressures and the adaptive value of the behavior to the organism. Given the enormous economic impact of acridid movements, it is of great practical importance to distinguish what factors are instrumental in the occurrence of migratory behavior.

The migrations of ***Melanoplus sanguinipes*** provide an interesting comparison with those of the more intensively studied Old World locusts. Like these locusts, ***M. sanguinipes*** engages in mass diurnal swarming during severe outbreaks. However, such swarming behavior has been reported only rarely in this century, always in association with unusual environmental conditions such as drought and high population density (Parker, Newton and Shotwell 1955; Scharff 1961).

VARIATION IN THE OCCURRENCE OF MIGRATION IN ACRIDID LIFE HISTORIES

Key (1945) proposed that acridids have dual habitat requirements: open ground for oviposition and vegetated areas for food and shelter. On this basis Southwood (1962) concluded that all acridids are therefore migratory. However, this greatly oversimplifies the problem. Many habitats may be considered as mosaics of vegetated and open areas, not requiring migration for the grasshopper or locust to obtain all needed resources (Dempster 1963). There is little published information available regarding the extent of intraspecific variability in migratory behavior in acridids despite considerable work on the development of locust outbreaks. Migration is not, however, associated exclusively with outbreaks.

For those species such as *S. **gregaria*** and *L. **migratoria***, possibly ***Oedaleus senegalensis*** (Riley and Reynolds 1983) and, historically, *M. **spretus*** (Riley, Packard and Thomas 1878, 1880 and 1884) which engage in "circuit" migration (Uvarov 1977), individuals travel between two habitats which become available at predictable and non-overlapping points in time (the same individual does not make the return trip although individuals of a subsequent generation do). In this situation, it seems likely that most if not all of the population moves with shifts of seasonal rain systems. However, the questions of whether some fraction of the population stays behind and whether there are variations in the distances traveled by individuals have not been specifically addressed. There is suggestive evidence for intra-population variability in ***Schistocerca gregaria*** in India (Ramchandra Rao 1942). Furthermore, in addition to the migrations of desert locusts between breeding zones in Africa, there is back and forth movement within a zone which is perhaps more extensive when population density is high (Kennedy 1956, Waloff 1966). There are also indications of geographical variation in migratory tendency between subspecies of ***L. migratoria*** outside of Africa, some of which have been observed to migrate only under exceptional conditions, as well as extensions of range that occur in the African population during outbreaks (see Uvarov 1977).

It is more common among acridids that the migrant does not travel in annual circuits, but moves away from the site of hatching in directions and at distances that may vary from year to year. In such migrations, annual periodicity is often difficult to detect since movements have generally not been reported unless the behavior is economically threatening (i.e., during high density outbreaks). Thus reliable information on annual variation in migratory behavior is not often available. Recent studies using radar tracking are beginning to address this problem (Riley and Reynolds 1983).

There is clear evidence from a variety of accounts of non-circuit locust movement and from recent work on ***M. sanguinipes*** that migration in such species need not be restricted to times of outbreak nor strictly dependent on population density. Chapman (1959), for instance, observed individual ***Nomadacris septemfasciata*** making long flights and noted that density seemed to have very little effect on flight. Migrations in the Australian plague locust, ***Chortoicetes terminifera***, occur virtually annually regardless of density (Farrow 1982). Evidence from recent field observations of the migratory behavior of ***M. sanguinipes*** indicated that even in the absence of mass flights, individuals in some populations take off on extended high altitude flights and that the proportion of migrants in such a population may be relatively high (Table 1). Thus, migration seems likely to be an annual event in a number of non-circuit migrants and can occur even in the absence of outbreaks or notable swarm behavior.

There also may be considerable geographic or temporal variation in the proportion of individuals within a species which engage in migratory behavior. This was illustrated by a comparison of three different populations of ***M. sanguinipes*** (McAnelly 1984). The first population was north of Ft. Collins, Colorado (the CO population), the second on the San Carlos Apache Indian Reservation in south central Arizona (the AZ population) and the third approximately 20 miles west of Silver City, New Mexico (the NM population). The extent of migration in the first two populations was assessed by direct observation and, in all populations, by testing the performance of field collected individuals in a stationary tethered flight assay.

Adult grasshoppers at the AZ site had been observed in mass migratory flight in 1980 (Pfadt 1982), and nymphs had been observed to engage in concerted marching behavior, a characteristic activity of migratory locusts (Uvarov 1977), in 1980, 1981 and 1982 (Foster, personal communication). Observations of individuals taking off, rapidly gaining altitude and flying beyond the range of binoculars were made in 1982 (McAnelly and Rankin, in preparation). In contrast, field observations at the CO site in 1980, 1981 and 1982, yielded no direct or indirect evidence of migratory behavior nor were there any published reports of migration at this site.

Direct evidence of migratory flight was not available for the NM site. However, this population was assumed to be migratory based on the observation that it had recently invaded an area previously devoid of grasshoppers. A tailings dam flood in October, 1980, covered 344 acres of ranch land with a thick sludge which destroyed anything not able to move out of its path. The tailings sludge was removed, and the area was covered with new topsoil and reseeded with grasses (Anonymous 1982). By

Table 1

Difference in flight behavior between field populations of ***Melanoplus sanguinipes*** (McAnelly 1984). There were no differences between males and females, therefore data were combined for sexes.

Flight duration (Minutes)	Arizona 1982	Colorado 1982	New Mexico 1983
0–55	109	141	21
56–60 +	43	7	29
% Migrant	28	5	58

χ^2 for Arizona vs. Colorado = 27.34, $p < 0.001$

χ^2 for New Mexico vs. Arizona = 14.53, $p < 0.001$

the summer of 1983 the site had been invaded by ***M. sanguinipes*** (McAnelly 1984). The grasshoppers were found closely associated with tumbleweed (***Salsoli kali***). Thus, insects found at the spill site in 1983 were either colonists or the progeny of colonists. In addition, ***M. sanguinipes*** was one of only two grasshopper species found within the spill area and comprised over 96% of all grasshoppers collected by sweep netting. Outside the spill area, species diversity was higher; ***M. sanguinipes*** comprised at most 62% of grasshoppers netted and was not the only species found feeding or roosting on tumbleweed.

In order to quantify migratory behavior in laboratory and field experiments, the stationary tethered flight assay devised by Dingle (1965) was modified for use with ***M. sanguinipes***. A tethered flight duration of 60 minutes was chosen as indicative of migratory flight behavior based on the probability that any given flight would still be in progress at a later time (McAnelly and Rankin, in preparation). In other words, initial studies with the assay showed that there is a high probability that any individual will cease flying before it has flown 60 minutes. However, having flown 60 minutes, it is likely to fly much longer (Fig 1).

Results of tethered flight assays of grasshoppers collected from each of the AZ and CO field populations and tested within 24 hours of capture were consistent with the previous assessments of the migratory tendency of each population in situ (Table 1). The NM field-collected grasshoppers had by far the greatest proportion of individuals that made a long-duration flight, indicating that this population indeed had a very high migratory capacity.

There can also be much temporal variation in the proportion of migrant individuals within a population of ***M. sanguinipes***. Although the Colorado population showed a relatively low degree of migratory behavior (Table 1), under certain conditions, the grasshoppers in this and similar habitats become highly mobile, with up to 90% of the population migrating (Parker et al. 1955).

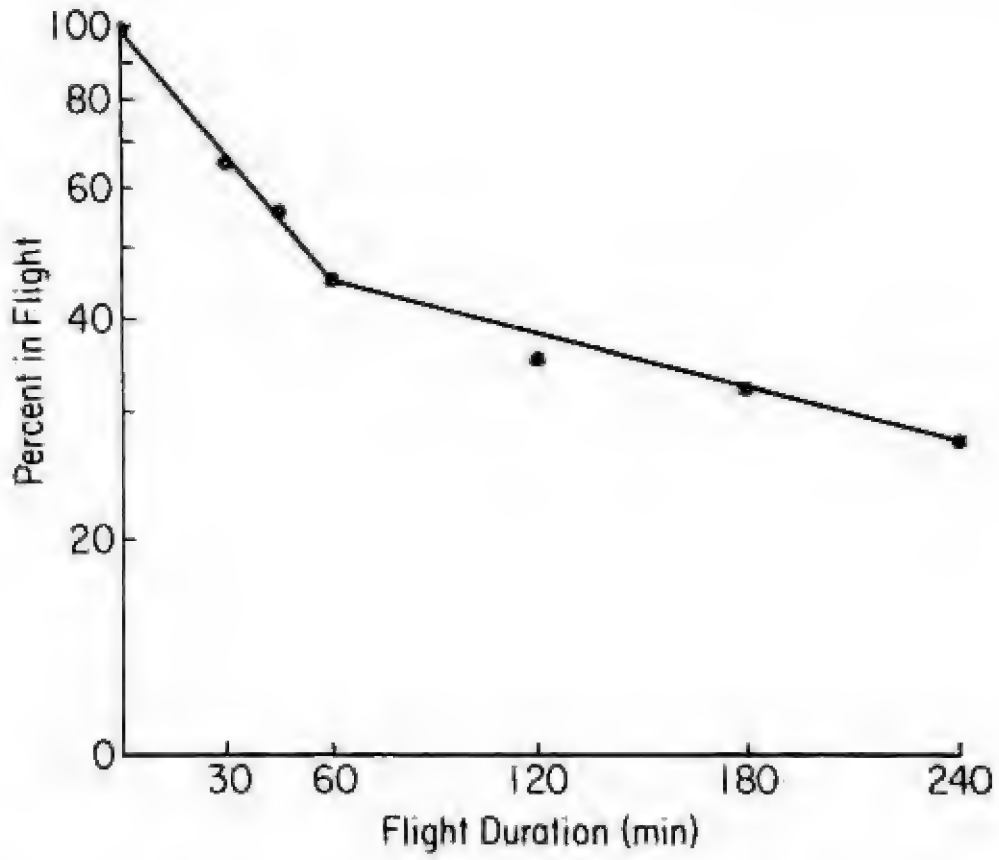

Figure 1

Log of the percent of grasshoppers in flight at a given time interval. n = 16 males and 16 females with a total of 66 flights.

Substantial individual variation in flight behavior was also observed. Even in a migratory (AZ) population, some individuals never undertook migratory flight, some did so once or twice, while many made long flights repeatedly (Fig 2).

MECHANISM OF VARIATION

There is evidence in many insect species that environmental parameters such as photoperiod, food quality, temperature, or density can alter the proportion of migrants in a population independently of any genetic change (Lees 1961, Dingle 1968; Rankin and Rankin 1980; Zera, Innes and Saks 1983; see also Rankin and Singer 1984). In other species, studies of the genetics of flight behavior and alary polymorphisms have indicated that flight tendency or the morphology necessary for migratory behavior can be inherited (Caldwell and Hegmann 1969, see Harrison 1980, Zera et al. 1983, Rankin, Singer 1984 and Zera, this volume).

In locusts, the phase theory (Uvarov 1921) focused attention on density as an important influence on many aspects of locust biology from morphology to physiology and behavior. For instance, locusts from low or high density populations (solitarious and gregarious phases, respectively) can be distinguished from each other physically on the basis of morphometric ratios and coloration (see Uvarov 1966). In laboratory experiments, isolated locusts are generally less active than crowded locusts (Ellis 1951) and tend to maximize their individual space, while gregarious locusts have a strong tendency to aggregate (Ellis 1953).

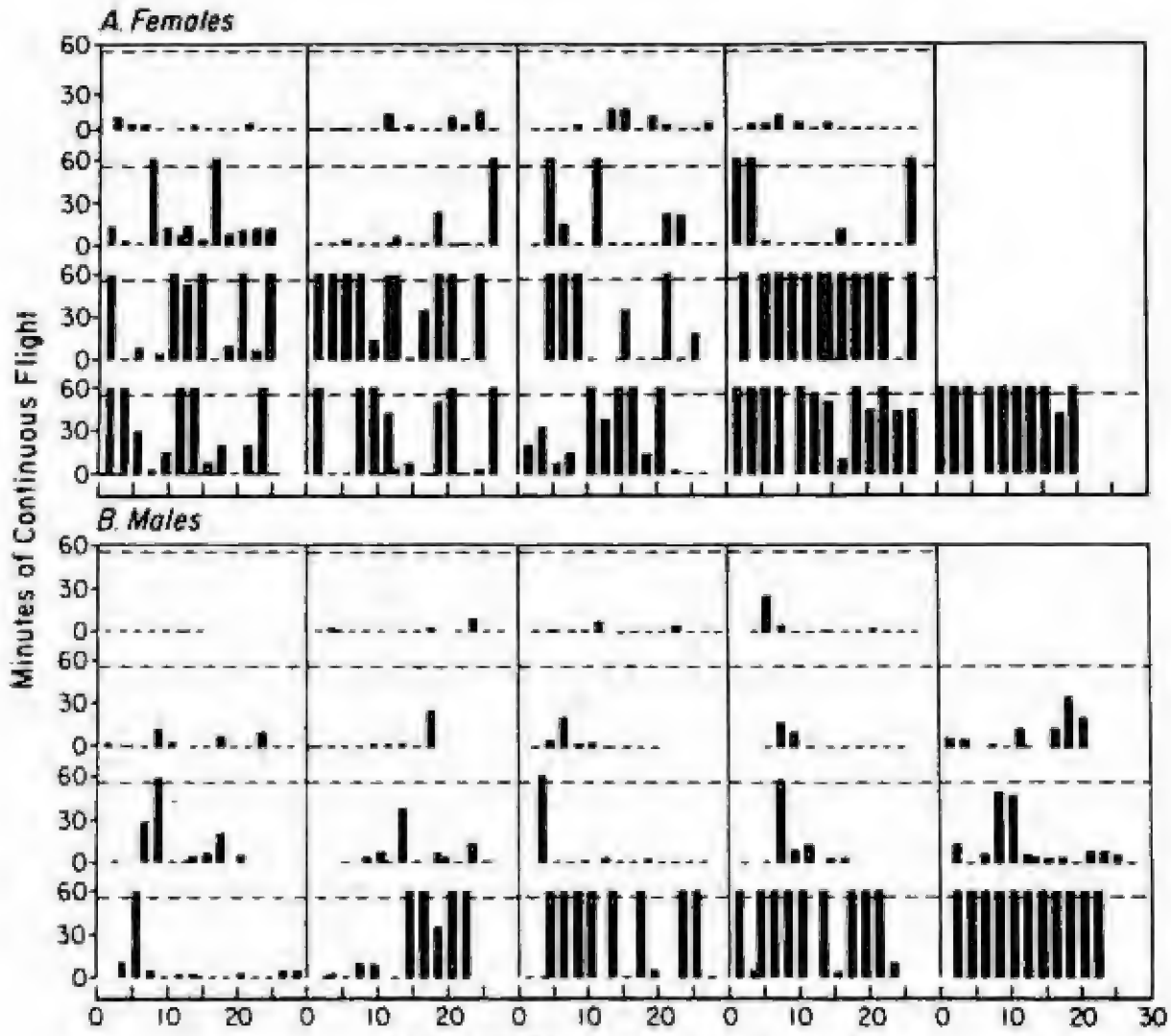
A. Females
B. Males
Minutes of Continuous Flight
60
30
0
0 10 20 0 10 20 0 10 20 0 10 20 0 10 20 30
Adult Age (Days after Adult Ecdysis)

Figure 2

Variation in flight performance of individuals. Animals were tested every other day between day 2 and day 28 after adult emergence. Flight durations were scored in 5 minute intervals, 0–5 to 55. Thus, dotted line at 55 minutes of flight represents criterion used to define migratory flight in this study. Each small square within frame A represents histogram of flight record for one female and within frame B, the histograms for each male.

The extent to which high population density can actually bring about a quantitative or qualitative change in locust migration is not precisely understood. Kennedy (1951a,b; 1956) proposed that migrations of outbreak populations were qualitatively different from the seasonal movements of solitary populations based on the cohesiveness of gregarious swarms and on their invasion of areas not normally part of the non-outbreak range. Michel (1970) compared the duration of flights made by isolated and crowded *S. gregaria* on round-abouts and found significantly less flight in isolated animals. The difference between isolated and crowded locusts was even greater in progeny from the respective parents, implying an acquired effect of density on flight behavior of subsequent generations.

In the field both solitarious and gregarious locusts make seasonal migrations; gregaria usually migrates during the day and solitaria at night (Davey 1953, 1959; Roffey 1963) although there are notable exceptions to even this dichotomy (Ramchandra Rao 1942, Roffey 1963). Although density can influence locust activity, it is not sufficient to account for all the observed variation in locust migratory

behavior.

The effects of temperature, photoperiod and relative humidity on flight behavior in locusts have been investigated in laboratory experiments. Crowded *L. migratoria* reared in decreasing photoperiod flew a greater number of revolutions on round-abouts than did those reared in increasing photoperiods (Albrecht and Michel 1975). However, in subsequent work on this species, increasing photoperiod produced the best flight performance (Lauga, Albrecht and Casanova 1982). Crowded *S. gregaria* flew best when reared under long day photoperiod and high temperatures (Michel, Albrecht and Casanova 1976) or increasing photoperiod (Albrecht et al. 1978).

There are difficulties in relating these results to field behavior. Firstly, the conditions correlated with greater flight in a given study were also correlated with improved ability to survive adverse conditions (Albrecht and Michel 1975). In addition, mortality from hatching to adult emergence was routinely 80%. Therefore it is not clear whether the parameter studied had a direct effect on flight or was simply producing healthier animals, nor to what extent differential mortality may have affected the results. Secondly, although gregarious locusts are in general diurnal migrants, all flight tests were conducted in total darkness. Finally, although locust migration may occur between bouts of oviposition, it is generally pre-reproductive (Johnson 1969), and flight is demonstrably greater in younger locusts (Lee and Goldsworthy 1976). The above tests on *Locusta* and *Schistocerca* were performed 48 hours after first oviposition in females without specifying the age of the locust for either males or females.

The question of whether environmental influences alter the expression of migratory behavior in *M. sanguinipes* is of particular interest in light of the inter- and intra-population variation observed in this species. However, there were no differences in flight performance between controls and experimental groups when the following were compared: photoperiod (16:8 versus 12:12 with adults maintained either at the nymphal photoperiod or switched on day of emergence); temperature (27°, 32° or 37°C); or the absence of fresh vegetation from the middle of the 5th instar through the adult flight testing period (McAnelly 1984). The lack of effect in the latter treatment is surprising compared with many insects in which starvation or declining food quality markedly increases flight behavior (Dingle 1968, Rankin and Rankin 1980) or conversely in which inadequate diet reduces tethered flight performance (Kester and Smith 1984, Davis 1984). However, migratory behavior in *C. terminifera* also seems to be relatively buffered against a wide range of change in food quality (Hunter 1982).

High density produced color changes in *M. sanguinipes* characteristic of phase polymorphism (Faure 1933, McAnelly, unpublished observations). However, its effects on flight behavior were equivocal. Grasshoppers were reared either in groups of 30, singly in the same environmental chamber as grouped animals or singly in a separate environmental chamber. Considering flight performance as a dichotomous trait in which "migrants" are defined as animals that made at least one 60 minute flight in 4 trials and "nonmigrants" as those that never made a long flight, there was no difference between either set of isolates and the grouped NM animals (Table 2A).

Table 2

Effects of density on flight behavior of laboratory-reared *M. sanguinipes* after adult emergence. Numbers of "migrants," defined as individuals which made at least one 60 minute flight in 4 trials, were compared between treatments as well as the overall frequency of long flight (the number of long flights in 4 trials for each animal). There were no differences between males and females, therefore the data are combined for the sexes.

A. NM "migrants"	Isolated in separate chambers	Isolated in same chamber as grouped animals	Grouped
No long flights	19	8	11
One or more long flights	30	13	40
	df = 2 χ^2 = 3.93 ns		
B. NM total numbers of long flights in all trials.			
Flights of < 60(fm	138	51	101
Flights >= 60′	58	33	103
	df = 2 χ^2 = 18.2 $p < 0.001$		
C. CO "migrants"	Isolated in separate chambers	Isolated in same chamber as grouped animals	Grouped
No long flights	8	18	25
One or more long flights	13	20	21
	df = 2 χ^2 = 1.58 ns		
D. CO total number of long flights in all trials			
Flights < 60′	64	114	146
Flights >= 60(fm	20	38	38
	df = 2 χ^2 = 0.96 ns		

However, if the total number of long flights made by all NM animals in 4 trials is analyzed, grasshoppers reared singly in a separate chamber made fewer total long flights than the grouped animals (Table 2B). No effect of density on either number of "migrants" or total number of long flights was seen in the CO animals whether

Table 3

Comparison of individuals making a 60 minute flight at least once in first generation lab-reared progeny of AZ and CO 1981 field parents. No difference was observed between males and females with respect to this measurement, therefore data by sexes were combined. All individuals tested every other day from day 2 to day 28 after adult emergence.

Number of 60 Minute Flights	AZ	CO
None	16	27
More than one	24	13
% Migrant	60.0	32.5

$\chi^2 = 6.08$, $p < 0.02$

isolates were reared in the same or a separate chamber from the grouped insects (Table 2, C and D).

That flight behavior or wing polymorphisms can be heritable has been frequently documented (Caldwell and Hegmann 1969, Zera et al. 1983, Harrison 1980, see Rankin, Singer 1984, and Zera 1985). However, the emphasis on density as a major factor in locust biology has deflected attention from the genetics of migration in acridids. Two lines of experimental evidence strongly indicate that the interpopulation variability in ***M. sanguinipes*** has a large genetic component. Firstly, in comparisons of first generation lab-reared progeny of AZ versus CO field parents (Table 3) and of 2nd, 3rd and 4th generation progeny of NM versus CO field parents (Table 4), the differences in flight behavior observed in the field were retained in the lab animals. Secondly, crosses between NM and CO lab animals indicated that these differences between populations were not due to a maternal effect. In both reciprocal crosses, flight behavior was virtually identical to that in progeny of the CO × CO cross and markedly different from those of the NM × NM cross (Table 5), suggesting that flight behavior in this species is heritable and somewhat recessive. Preliminary results from within population crosses of flyers and non-flyers indicate that there is also likely to be a strong genetic influence on the within-population variability (McAnelly 1984).

Evidence from field observations also suggests that migratory behavior in ***M. sanguinipes*** may be under strong genetic influence. Nymphs hatching from eggs laid by immigrant females during the outbreak of the late 1930's were distinctly more migratory than nymphs in nearby localities in which flights had not occurred for several years (Parker et al. 1955). In addition, migrations in this outbreak did not begin until after at least 4 years of severe drought and population increase. Such a time lag could have been sufficient for (though certainly does not necessitate) selection to have produced the dramatic increase in the proportion of migrants within a

Table 4

Comparisons of the number of "migrants" (individuals that made at least one long flight in four trials) in 2nd, 3rd, and 4th generation lab-reared progeny of NM and CO field parents. First generation progeny were not available for simultaneous comparison. These comparisons are drawn from control animals used for other experiments (examination of the effect of photoperiod, density, etc.). In each generation the CO and NM grasshoppers compared were reared at the same time under the same conditions.

	2nd generation*		3rd generation		4th generation	
	NM	CO	NM	CO	NM	CO
No long Flights	5	41	0	25	4	11
One or more long flights	82	45	52	21	35	16
% migrants	94.3	52.3	100	45.6	89.7	59.3
	$\chi^2 = 38.81$ $p < 0.001$		$\chi^2 = 38.20$ $p < 0.001$		$\chi^2 = 8.59$ $p < 0.01$	

*Reared under a variety of photoperiods. No effect of any photoperiod on flight, therefore all data were combined.

population.

ADAPTIVE VALUE OF MIGRATION

Many acridids are inhabitants of semi-arid to desert environments in which lack of rainfall is a major obstacle to survival. It is not surprising to find that migrant locusts often take off on and travel with convergent wind systems which are likely to deposit an organism in an area where rainfall will soon occur (Rainey 1951). The seasonal movements of *S. gregaria* and *L. migratoria* have clear adaptive value; the insects alternate between two ephemeral breeding habitats that reappear predictably each year (Waloff 1946). Even when migration is more nomadic than circuitous, by riding appropriate weather fronts, a locust such as *C. terminifera* is also likely to arrive at a site where rainfall and growth of fresh vegetation will soon occur (Clark 1969).

In those acridids such as *M. sanguinipes* in which there is considerable temporal and geographic variation in the frequency of migrants, the role of migration in the species' ecology may be more complex and may depend upon the quality of a particular habitat.

Table 5
Comparison of flight performance of the progeny of crosses between CO and NM grasshoppers.

	CO × CO	NM × CO	CO × NM	NM × NM
No long flights	11	12	34	4
One or more long flights	16	16	51	35
% migrants	59.3	57.1	60.0	89.7

$\chi^2 = 12.71, p < 0.01$

Comparison of the AZ and CO sites in this study revealed important habitat differences. Both receive approximately equal rainfall (37 cm), but maximum daily temperatures are higher in Arizona (36−38°C versus 27−30°C); this, along with lack of irrigation or surface water on the San Carlos Reservation and differences in land use practices combine to produce a far more xeric environment at the AZ site. In addition, there is a marked dry season at the AZ site with virtually no precipitation from April until mid- to late July. When late summer rains begin, they are most likely to occur as highly scattered thunderstorms. Areas of fresh green vegetation which arise in response to late summer rainfall are, as a result, quite patchily distributed.

These aspects of habitat quality have several important consequences for ***M. sanguinipes***. Although this species is a generalist feeder, forage conditions on the San Carlos Reservation can easily become too limited to support growth of nymphs by mid-summer. Even if dried senescent vegetation were still available, some factor or factors in fresh green plant material appear to be necessary for nymphal growth (Kreasky 1962). Finally, survival of eggs requires a soil moisture of at least 13.5% (Mukerji and Gage 1978). By mid-July, soils on the San Carlos Reservation lack even this minimal amount of moisture at oviposition depth.

Migration in the AZ population, therefore, is likely to increase the chance that individuals will find patches suitable for reproductive maturation, oviposition and development of nymphs. The presence of a significant fraction of nonmigrants in this population may reflect the probability that the natal habitat will occasionally receive adequate rainfall.

At the CO site, green vegetation is normally available throughout the summer. Individuals probably do better on average by taking advantage of locally favorable conditions than by emigrating. However, at unpredictable and infrequent intervals, droughts of extended duration occur in this region, accompanied by an increase in the proportion of migrants (Parker et al. 1955). In the CO habitat therefore, migration permits ***M. sanguinipes*** to escape sporadic periods of unusually xeric conditions.

Melanoplus sanguinipes occurs throughout most of the USA but is particularly abundant in disturbed habitats, i.e., areas in which crops or native grasses have been replaced by weeds, often non-native plants (Parker et al. 1955, Pfadt 1982). As a result of the tailings dam flood described above, the NM site was an extreme example of a disturbed habitat which *M. sanguinipes* was able to invade and exploit. While this particular colonization need not have involved exceptionally long-distance movement, it demonstrates the remarkable opportunism typical of migrant insects in general (Southwood 1962, Parsons 1982). The ability to find and move to such a resource could have considerable adaptive value regardless of the quality of the original habitat.

CONCLUSIONS

The existence of inter- and intra-population variation in flight behavior and the genetic basis for this variation implies that formation of swarms in *M. sanguinipes* may be strongly driven by selection pressures acting over a few generations. Increased population density during outbreaks could intensify the migratory response, but is not likely to be the primary causal factor.

These results do not refute the importance of high density to the dynamics of locusts plagues. *Melanoplus sanguinipes* may have a different behavioral response to crowding. It is not known, for instance, whether this species is capable of exhibiting increased aggregation behavior in response to crowding as is seen in the locusts. Further, Kennedy's comment (1951a, p. 230) regarding the importance of high density locust plagues may apply equally well to *M. sanguinipes* swarms: "We may reasonably infer that the migration of these insects would be less persistent, if they did not move in compact, 'disciplined' armies. If they did not migrate in this way, be it noted, they would lose their uniquely catastrophic character as pests of crops." However, it is clear that genotype is a potentially critical factor in the migration of acridids and that this should be carefully examined in other species, using field animals or those recently derived from field populations if possible.

The existence of genetically determined migrants implies that even in a relatively sedentary population there are individuals capable of taking advantage of newly available habitat. As suggested by work on the NM population, the ability to invade and exploit disturbed habitat may be quite important. A high intrinsic rate of increase (Pfadt and Smith 1972), generalist food preferences and the ability to live in a wide range of environments as indicated by its distribution (Gurney and Brooks 1959) distinguish this organism as a classic colonist as described by Parsons (1982). This, in conjunction with its migratory behavior, make it likely that even in normally "lush" environments such as the CO site, *M. sanguinipes* can do well by moving to and exploiting areas of disturbed habitat. Such habitat will be created frequently through human activities (mowing roadsides, overgrazing, etc.) or natural events, thus favoring some rate of production of colonists and opposing selection pressures against migratory behavior. Alexander (1951) observed that *M. sanguinipes* near Boulder, CO is found outside of its normal altitudinal range almost annually and suggested that

movements beyond the animal's central range act to expand the borders of the range in those years when the quality of marginal habitat is improved. Thus unusual environmental conditions are not necessarily a prerequisite for the production of migrants.

These results also suggest that human activities which disrupt habitat may help maintain migratory behavior even in the face of counteracting selection for sedentary individuals. Historically, outbreaks and invasions of locusts and grasshoppers have been linked to human disruption of habitat (Roffey 1972). Conversion of forested areas in Australia to grazing lands allowed expansion of *C. terminifera* (Farrow 1979) into new areas. The latter remains a serious agricultural problem in New South Wales, and migratory behavior seems to be maintained here at least in part by continual re-invasion of locusts from other regions. During settlement of the great plains, grasshopper outbreaks and migrations occurred at regular intervals (Riley, Packard and Thomas 1878, 1880, 1883). It is quite likely that conditions created by settlement and destruction of the prairies with concomitant introduction of European weeds (such as *Salsoli kali*) increased the rate of formation of disturbed habitat which may in turn have favored both population increase and selection for highly migratory grasshoppers during this period.

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BUTTERFLY MIGRATION IN THE BOUNDARY LAYER

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ABSTRACT

Long-distance aerial migration by insects is usually at altitudes where wind speeds exceed air speeds of the migrants, restricting their possible tracks to the direction of the wind ± 90°. However, migrating butterflies generally fly near the ground where wind speeds are low enough to permit progress in any direction. Three species of such boundary-layer migrants are conspicuous in southeastern United States each fall: ***Phoebis sennae*** (cloudless sulphur), ***Agraulis vanillae*** (gulf fritillary) and ***Urbanus proteus*** (long-tailed skipper). Migrants fly in a straight line within a few meters of the surface. At a given locality their tracks usually cluster about a single direction. Based on observations at Gainesville, Florida, mean direction changes little with time of day, season, or direction of wind. Mean direction changes significantly with geographical locality in a pattern which suggests navigation by the butterflies and a destination of peninsular Florida. For example, in northern Alabama and Mississippi the mean direction of ***P. sennae*** is ca. 135°, whereas in south-central Georgia it is ca. 155°, and near the Atlantic coast in south Georgia and north Florida it is ca. 175°. Migrants moving down the Florida peninsula each fall may number 11−16 million ***A. vanillae***, 29−48 million ***P. sennae*** and 41−396 million ***U. proteus***.

INTRODUCTION

Most migrating insects fly at altitudes where wind speed exceeds their air speed (Johnson 1969). Consequently, their direction of movement must fall within the semicircle toward which the wind is blowing. Radar studies generally show that high altitude migrants are flying with the wind—i.e., their heading approximates the direction of the wind, and their velocity approximates the sum of their air speed and the wind speed (Pedgley 1982).

On the other hand some insects migrate in their ***boundary layer***, the layer of air near the ground where wind velocity is less than the insects' air speed. The thickness of the boundary layer for a particular migrant depends not only on the profile of wind speed vs. height but also upon what air speed the migrant can maintain (Taylor 1958, Pedgley 1982). Insects in their boundary layer can progress in any direction and are

generally close enough to the surface to make feasible their study by direct observation.

Butterflies are the best known boundary-layer migrants among insects (Williams 1930, 1958; Baker 1978). Most species can be identified in flight, and individuals can be followed visually far enough to yield a reliable measurement of the migrant's track. In southeastern United States at least eight species of butterflies migrate southward each fall (Walker 1978, 1980; Urquhart and Urquhart 1978). This paper deals with the three that are especially abundant and easy to recognize in flight: ***Phoebis sennae*** (cloudless sulphur), ***Agraulis vanillae*** (gulf fritillary) and ***Urbanus proteus*** (long-tailed skipper).

GENERAL ASPECTS OF MIGRATION

During winter each of the three species is restricted, in eastern United States, to a small portion of its summer range. ***A. vanillae*** and ***U. proteus*** overwinter only in peninsular Florida and ***P. sennae*** only in the Gulf region. During summer they move northward, regularly breeding at least as far north as Kansas and Virginia (Walker 1978). The movement northward each spring is seldom discernible, but provided the contrast between summer and winter ranges is correct, it must occur. The movement southward each fall is often conspicuous and can be regarded as a flight toward suitable overwintering grounds.

Observable fall flight paths of ***P. sennae***, ***A. vanillae*** and ***U. proteus*** are remarkably straight. Typically, from the time the butterfly comes into view until it disappears, its track changes no more than a few degrees. When the migrant encounters an obstacle such as a building or a dense wood, it flies up and over rather than deviating to either side. Over open ground, migrants seldom fly higher than 2 m (Fig 1).

The low height of flight and the behavior of migrants when they encounter a barrier make it feasible to construct flight traps that catch migrants and that keep separate those migrants that encountered the trap from one direction (± 90°) and those that encountered it from the opposite direction (± 90°) (Walker 1978, 1980). I have operated such traps at Gainesville during seven falls and seven springs. The traps are oriented perpendicularly to the axis of the Florida peninsula in order to distinguish migrants flying down the peninsula from those flying toward Georgia. For ***P. sennae***, ***A. vanillae*** and ***U. proteus*** the traps have documented large-scale fall flights southward; for ***P. sennae*** and ***A. vanillae*** they have revealed small-scale spring flights northward (Table 1).

The numbers of migrants fluctuate substantially from one fall to the next. Documentation of this annual variation comes from operating the same 6-m long, 3-m high hardware-cloth flight trap at the same site for five years (1979−83) (see Fig 5B in Walker 1980). The numbers of fall migrants were lower in 1983 than for any previous year (Fig 2). This pattern correlates with record droughts in the northwestern portion of the summer breeding area.

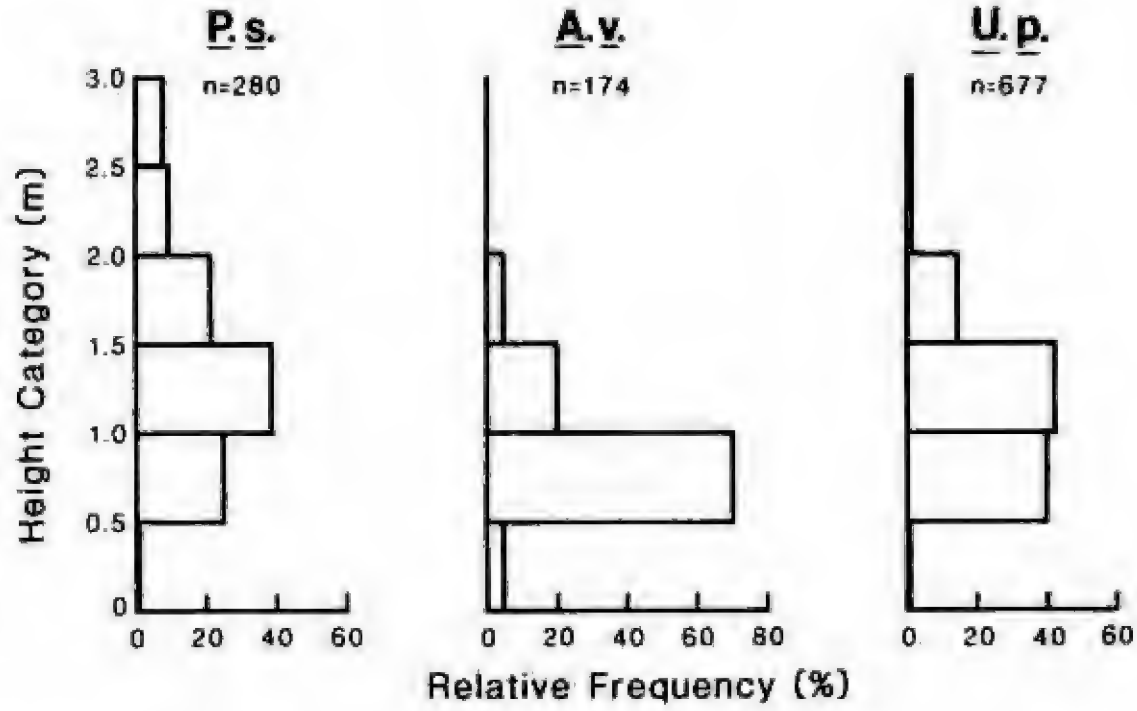

Figure 1

Frequency distribution of heights of three species of butterflies migrating across an open field, Gainesville, Florida, 31 Aug–12 Oct 1983. Uppermost category includes all individuals flying above 2.5 m. *P.s.* = *Phoebe sennae*, *A.v.* = *Agraulis vanillae*, *U.p.* = *Urbanus proteus*. (Heights were recorded as migrants flew between 3-m tall poles which were marked at 1-m intervals; 15-min observation periods began at 1130 and at 1230 h LMT, 3 days per week.)

The timing of fall flights through Gainesville were similar each year, and differences among the three species were minor (Fig 3). The flights start in early September and conclude in early November. Approximately 50% of the fall migration occurs between mid-September and mid-October (see also, Walker and Riordan 1981).

Nearly 50% of fall migrants at Gainesville are males, and 20–80% of the females have already mated at least once (Walker 1978). Mean air speed of migrants has been measured at 4.8 *(A. vanillae)* to 6.1 $m \cdot s^{-1}$ *(U. proteus)* (Arbogast 1966, Balciunas and Knopf 1977).

DIRECTIONS OF FALL MIGRANTS: EXPERIMENTAL PLAN

Butterflies that breed in areas as widely separated as Kansas and Virginia must find their way to common winter ranges or perish. For example, *A. vanillae* and *U. proteus* in eastern United States survive winters only in south Florida. The study here reported was designed to monitor directions of fall flights throughout the summer breeding ranges to learn whether migrants have a common destination, and if so, what routes are taken to it.

Widespread monitoring of flights on a modest budget requires that observations at an average site be limited to one or a few dates, times of day and weather conditions. Yet it is important to know whether these variables affect the directions taken by fall migrants. Consequently I divided my efforts into two components: (1) brief observations of directions at many localities which collectively represented as much of the summer breeding ranges as I could reach and (2) intensive study of directions at Gainesville, where observations could be made at all times of season and

Table 1
Direction of flights as revealed by catches in flight traps perpendicular to the axis of the Florida peninsula, Gainesville, Florida, 1975–1983.

Species	Fall			Spring		
	North-flying	South-flying	% S	North-flying	South-flying	% N
Phoebis sennae	165	2186*	93	19**	1	95
Agraulis vanillae	28	757*	96	16**	2	89
Urbanus proteus	92	3562*	97	1	1	50

* Directions of fall flights biased southward ($p_\alpha < 0.005$).

** Directions of spring flights biased northward ($p_\alpha < 0.005$).

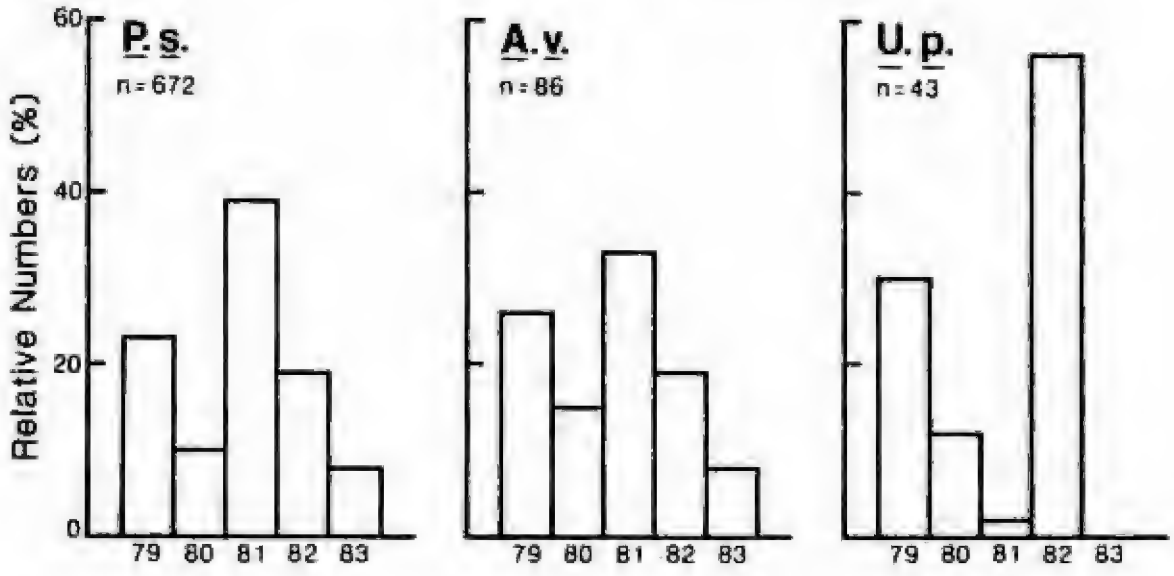

Figure 2
Annual changes in numbers of three species of fall migrants, Gainesville, Florida, 1979–1983, based on catches of one permanent flight trap; data are expressed as percent of 5-year catch. (Total catch of *U. proteus* is low because trap efficiency for that species is close to nil; indeed none were caught in 1983.)

day and under a full spectrum of weather conditions. The hope was that by thoroughly understanding fall directions at one site, scant records from other sites could be correctly interpreted.

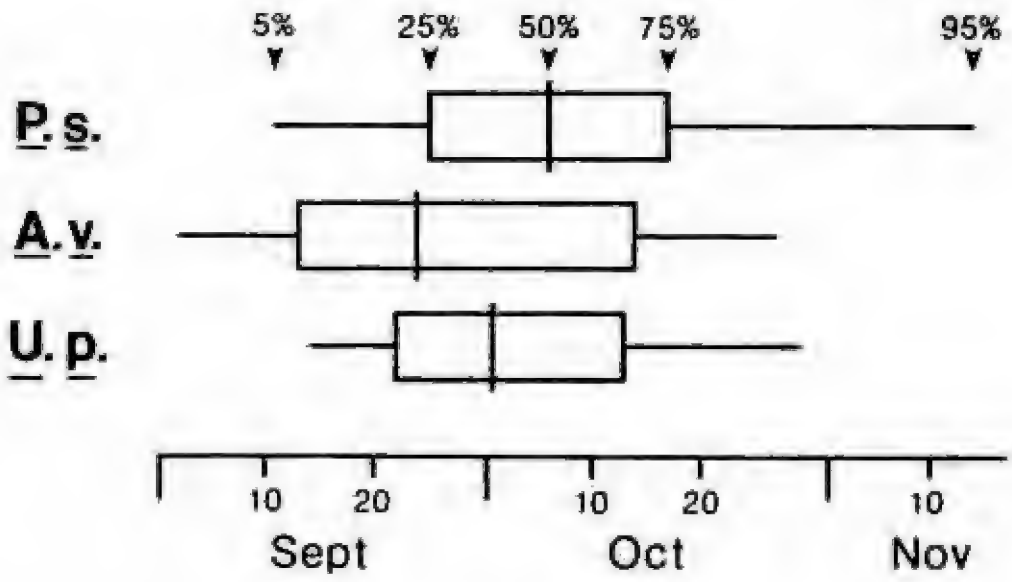

Figure 3

Average progression of fall migration as revealed by flight-trap catches, Gainesville, Florida, 1978–83. Vertical line is date that median migrant was caught; horizontal bar is middle 50% of migration; horizontal line is middle 90%. Differences between species were not consistent from year to year except that *A. vanillae* migration reached 5 and 25% completion earliest and *P. sennae* reached 95% latest. (Total samples: *P. sennae* = 748, *A. vanillae* = 244, *U. proteus* = 1057.)

DIRECTIONS AT GAINESVILLE

Methods

All observations of flight directions at Gainesville were made in the central portion of a 8-ha bahiagrass field at University of Florida's Green Acres Farm (29°41′N, 82°30′W). Preliminary observations were made Oct 1982. In 1983, two assistants alternated in measuring migratory directions each Monday, Wednesday, and Friday, 31 Aug to 11 Nov 1030–1330 h LMT (local mean solar time, based on local longitude). (At Gainesville, LMT = EDT (eastern daylight time, based on 15° time zone) −90 min). The procedure for determining a migratory direction was to spot a straight-flying butterfly, walk or run to where it had just been, and with a sighting compass (SUUNTO KB-14) read the magnetic bearing of its direction of disappearance. In addition to magnetic bearing (later converted to true bearing) the following data were noted for each record of migratory direction: time (standard time, later converted to LMT), species, blue sky visible (% of total), appearance of sun (disc bright, hazy, obscured or partly obscured), wind direction (as indicated by a 0.3-m plastic ribbon dangling from the ring end of a horizontal laboratory thermometer attached at 1 m to a slender post), wind speed (as measured by a Dwyer pith-ball anemometer) and air temperature at 1 m (the thermometer bulb was shaded by a plastic shield, 3-cm dia. × 10 cm).

As soon as a record was entered on the data sheet, visual search for another migrant began. At times of peak migration as many as 80 records were taken in an hour. Bias in selecting butterflies for observation was minimized by scanning perpendicular to the approximate axis of migration and selecting the first straight-flying butterfly whose path could be reached.

On six days, migration directions were measured during the entire period of migration (ca. 0800–1700 h LMT). Migratory directions were grouped by species, time of season, date, and time of day, and the following statistics calculated: mean direction (M.D.), length of mean vector (*r*), 95% confidence interval of M.D. (Batschelet 1981).

Results

Time of Season — Mean migratory directions remained approximately the same throughout the season and were similar for the three species (Figs 4,5). The principal difference among species was that during the first two-thirds of fall migration the distribution of *A. vanillae* directions was bimodal, whereas *P. sennae* and *U. proteus* each manifested a single mode of migratory direction throughout the fall. Their single modes approximated 141°, as did the greater of the two *A. vanillae* modes (Fig 4). The minor *A. vanillae* mode (ca. 63°) was not evident after 14 October.

During the first few weeks of migration, directions of *P. sennae* were more variable than during the remainder of the season, as shown by the *r* values and (for given sample sizes) confidence intervals (Figs 4, 5). (No confidence intervals were calculated for *A. vanillae* mean directions during the first 7 weeks because the assumption of a circular normal distribution was violated.)

Time of Day — All records of directions summarized in Figures 4 and 5 were taken during 1030–1330 LMT. Whether mean direction changed with time of day was addressed by pooling observations at hourly intervals for the six days of daylong observation (Fig 6). No temporal trends are evident in *U. proteus* or *A. vanillae*. *P. sennae* was more variable, but only one hourly M.D. was significantly different from 141°.

Crosswinds — When butterflies encounter crosswinds, they can sometimes be seen to turn their headings toward the wind—a behavior that reduces or negates drift (Williams 1958). The effects of crosswinds on fall migratory direction of *P. sennae* and *U. proteus* at Gainesville were judged by comparing directions on days with right and left crosswinds. Only two days (5 Oct, 4 Nov) had large numbers of migrants and consistently left (NE) crosswinds (Fig 7). *P. sennae* did not fully compensate, but *U. proteus* apparently did. (*A. vanillae* was not analyzed because numbers were low and the distribution of migratory directions was sometimes bimodal.)

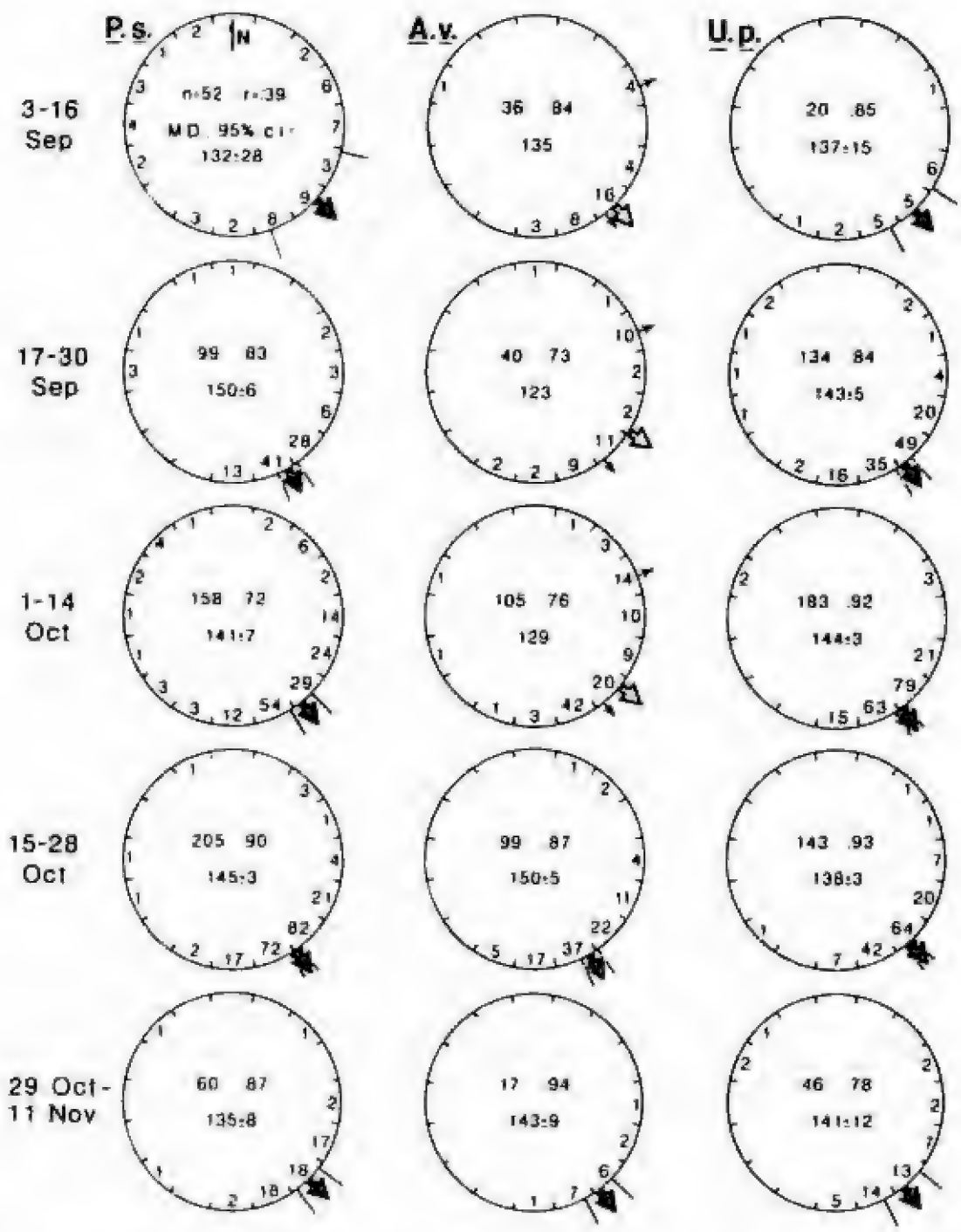

Figure 4

Directions of fall migrants, biweekly periods, Gainesville, Florida 1983 (1030–1330 h LMT). Within each circle are frequency distributions of true bearings (grouped at 22.5° intervals), number of observations, length of mean vector (*r*), mean direction (M.D.) and, where frequency distribution is appropriate, 95% confidence interval of M.D. Outside each circle is an arrow indicating mean direction and, where appropriate, lines defining the 95% confidence interval. For first three biweekly periods of *A. vanillae*, small arrows indicate estimated directions of the two modes (viz. 63° and 141°).

Discussion

With some noteworthy exceptions, mean directions of fall migrants at Gainesville remained close to 141° regardless of species, time of season, time of day, or wind. If I had recorded migratory directions at Gainesville for only a few hours on one or a few dates, the mean migratory directions of any of the three species would likely have been ca. 141° but could have deviated from that value by 10 or more degrees.

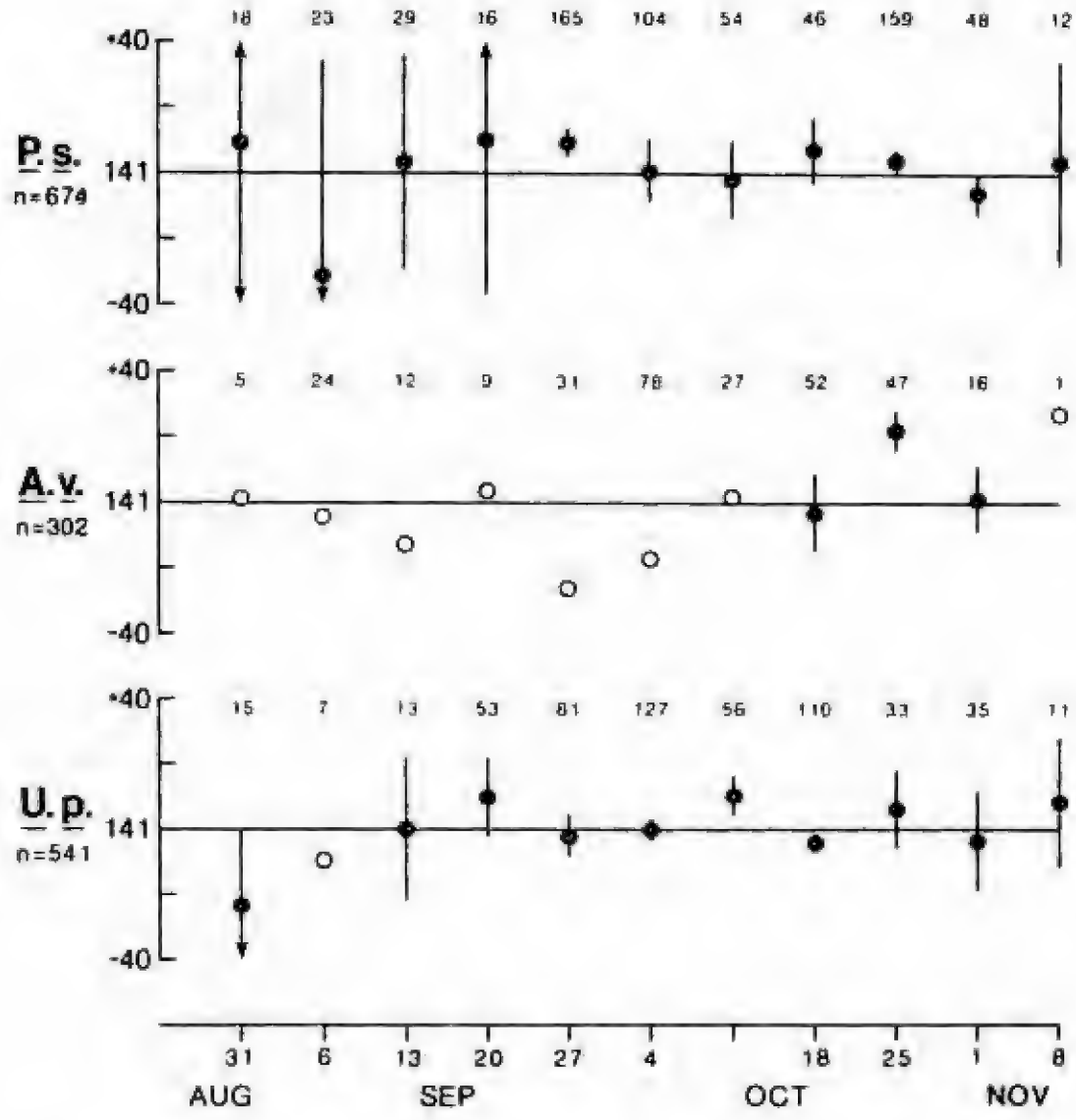

Figure 5

Direction of fall migrants, weekly periods, Gainesville, Florida, 1983 (1030–1330 h LMT). Each dot shows mean direction relative to 141°. Sample size is above each dot. For solid dots, vertical line shows 95% confidence interval (arrows indicate that c.i. exceeds the limits of the graph). Open dots indicate that distribution of directions was bimodal or that *n* was too small to determine a confidence interval.

The early season bimodality of *A. vanillae* directions at the Gainesville site is unexplained. No minor mode was evident in records made during pilot studies in 1982 nor at other localities in 1983. Minor mode directions were especially prevalent during midday, a time that corresponds to a decline in migratory activity (Fig 8).

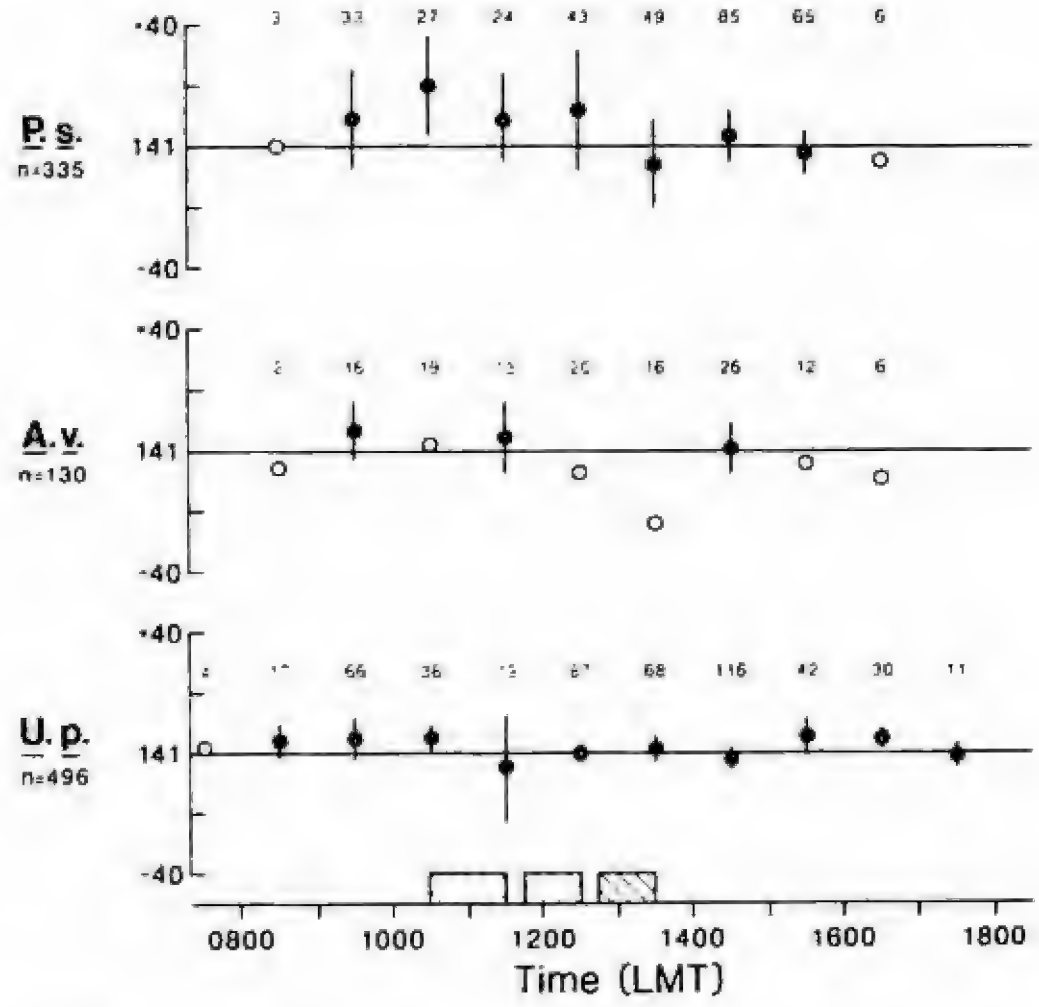

Figure 6

Direction of fall migrants, hourly periods, Gainesville, Florida; 3, 11, 15 Oct 1982; 3, 4, 7 Oct 1983. Same conventions as Figure 5. Hatched areas at bottom show times of observation for Figures 4, 5, 7.

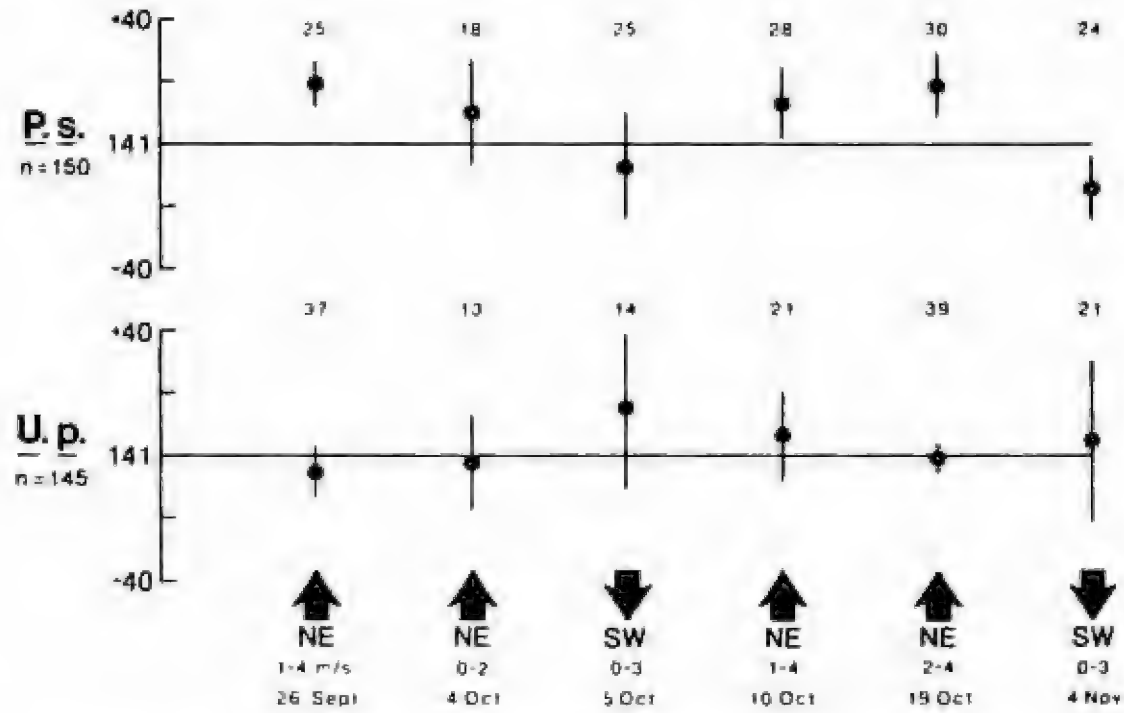

Figure 7

Mean directions and 95% confidence intervals of *P. sennae* and *U. proteus* in left (NE) and right (SW) crosswinds, Gainesville, Florida, 1983 (1030–1330 h LMT). Arrows above wind information show direction of effect of wind if migrants do not fully compensate.

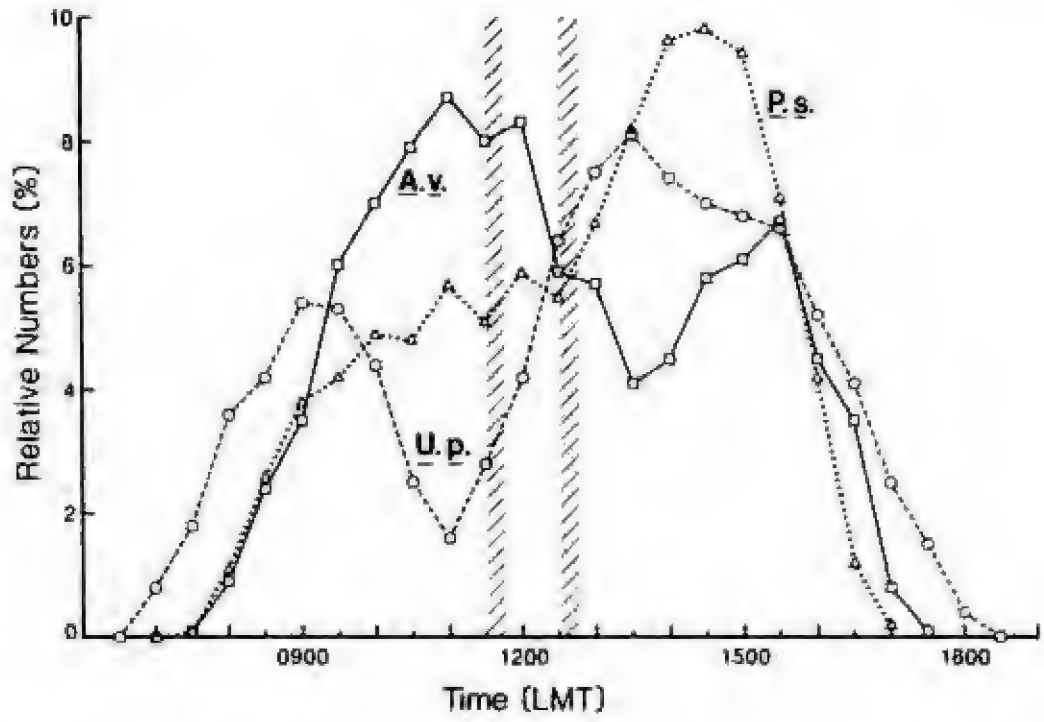

Figure 8

Half-hourly trends in numbers of migrants, based on counts during 4 days (11, 15 Oct 1982; 3, 4 Oct 1983) at Gainesville, Florida Hatched bars show 15-min periods during which routine counts of migrants were made during fall 1983 (see Table 2). Moving three-point average was used to smooth data for each day and the values plotted here are the averages of the normalized data for each of the four dates.

DIRECTIONS ELSEWHERE

Literature Records

P. sennae are brilliant yellow and therefore conspicuous in their migratory flights. This has contributed to there being a significant number of published reports of directions of their fall flights (Fig 9). A remarkable feature of these reports is that they agree that the flight direction is "southeast" (no further quantification) when the locality is inland and that the direction is coastwise when the locality is near the coast. A map of the records (Fig 9) suggests this hypothesis: *P. sennae* (and perhaps *A. vanillae* and *U. proteus)* from all over southeastern United States arrive at suitable overwintering grounds by flying southeast until they reach a coastline. They then follow the coast (with an eastward or southward component if they are to reach peninsular Florida). Specimens that head northward along the north Atlantic coast are probably doomed—and especially likely to be reported (e.g., Muller 1977, Pyle 1981).

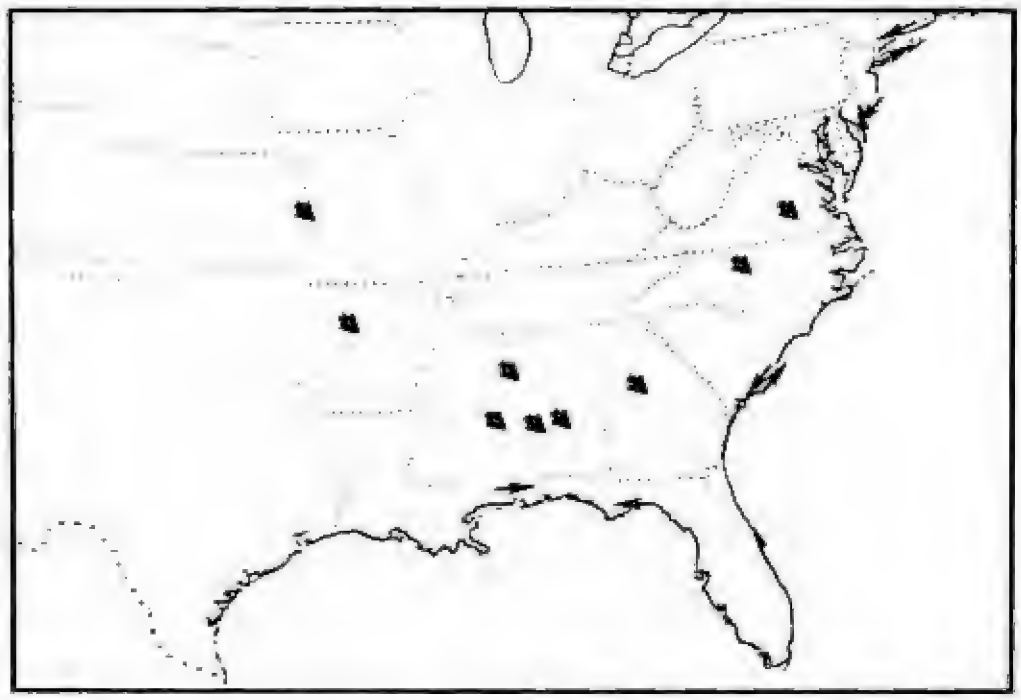

Figure 9

Literature records of direction of fall migration of *Phoebis sennae* (Shannon 1916; Williams 1930, 1958; Clark and Clark 1951; Lambremont 1968; Howe 1975; Urquhart and Urquhart 1976; Muller 1977; Gaddy and Laurie 1983). Inland, the direction has always been southeast; coastal records have been parallel to the coast.

Methods

During fall 1982 and 1983, 30 localities in southeastern United States were visited one to four times to observe directions of migrating butterflies (Fig 10). Localities were generally established at intervals of ca. 100 km along east-west lines. At each locality an observation site was selected for its openness, extent and accessibility. Playing fields and school campuses were frequent choices. If a site better than the one first chosen was subsequently found, observations were thereafter made at the new site. All sites were at least 10 km from the coast and salt-influenced communities.

Flight directions were generally determined in the same manner as at the Gainesville (GVL) site. However, when migrants were scarce, the number of records was increased by this procedure: if a butterfly was spotted close enough to watch but too far to reach, a line was estimated parallel to the flight path of the migrant and its azimuth was measured. Directions taken in this manner did not differ significantly in mean direction from those taken (at the same site and observation period) by reaching the flight path of the migrant.

Dates, times and conditions of observation and numbers of records by species are given in Appendix 1.

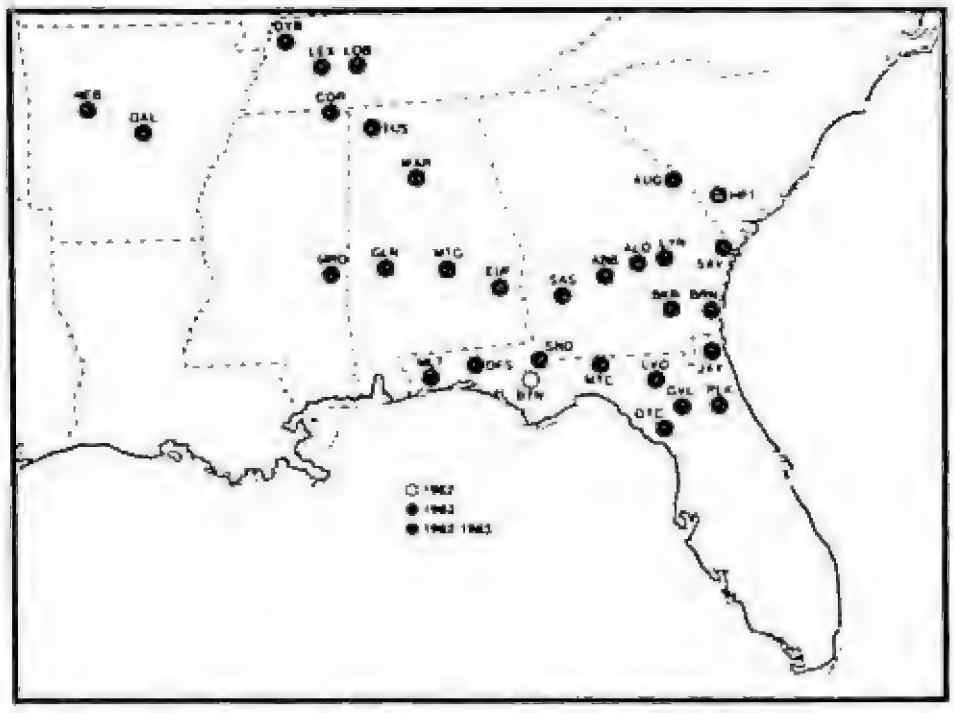

Figure 10
Localities for observing fall migrations, 1982–83.

Results

Results are detailed in Appendix 2 and summarized (for *A. vanillae* and *P. sennae*) in Figure 11.

Only the data for *P. sennae* are geographically extensive. Mean flight directions for northern Mississippi (COR), northern Alabama (TUS) and central Alabama (MTG) were 133 ± 3, 136 ± 4 and 138 ± 5, respectively. On the other hand, mean directions in central Georgia (ABB, ALO, LYN) were 154 ± 10, 152 ± 5 and 160 ± 12. Finally, mean directions in southeast Georgia (BRN) and northeast Florida (JAX) were 185 ± 11 and 163 ± 4. With the exception of two west Tennessee localities (DYB, 166 ± 14; LEX, 153 ± 14), mean directions for *P. sennae* were essentially toward the Florida peninsula. Data for *A. vanillae* (Fig 11) and *U. proteus* (Appendix 2) are similar to the *P. sennae* data but are restricted to localities in north Florida and south Georgia.

Discussion

The hypothesis that all inland fall flights are in the same direction is refuted and an alternative hypothesis is supported—viz. that inland flights are principally toward peninsular Florida.

Earlier records for *P. sennae* migrations agree with the new hypothesis as well as with the old, except records in North Carolina (Shannon 1916, p. 228; arrow on map, no numbers) and Virginia (Clark and Clark 1951, p. 114; "many individuals of this species all flying toward the southeast across the road").

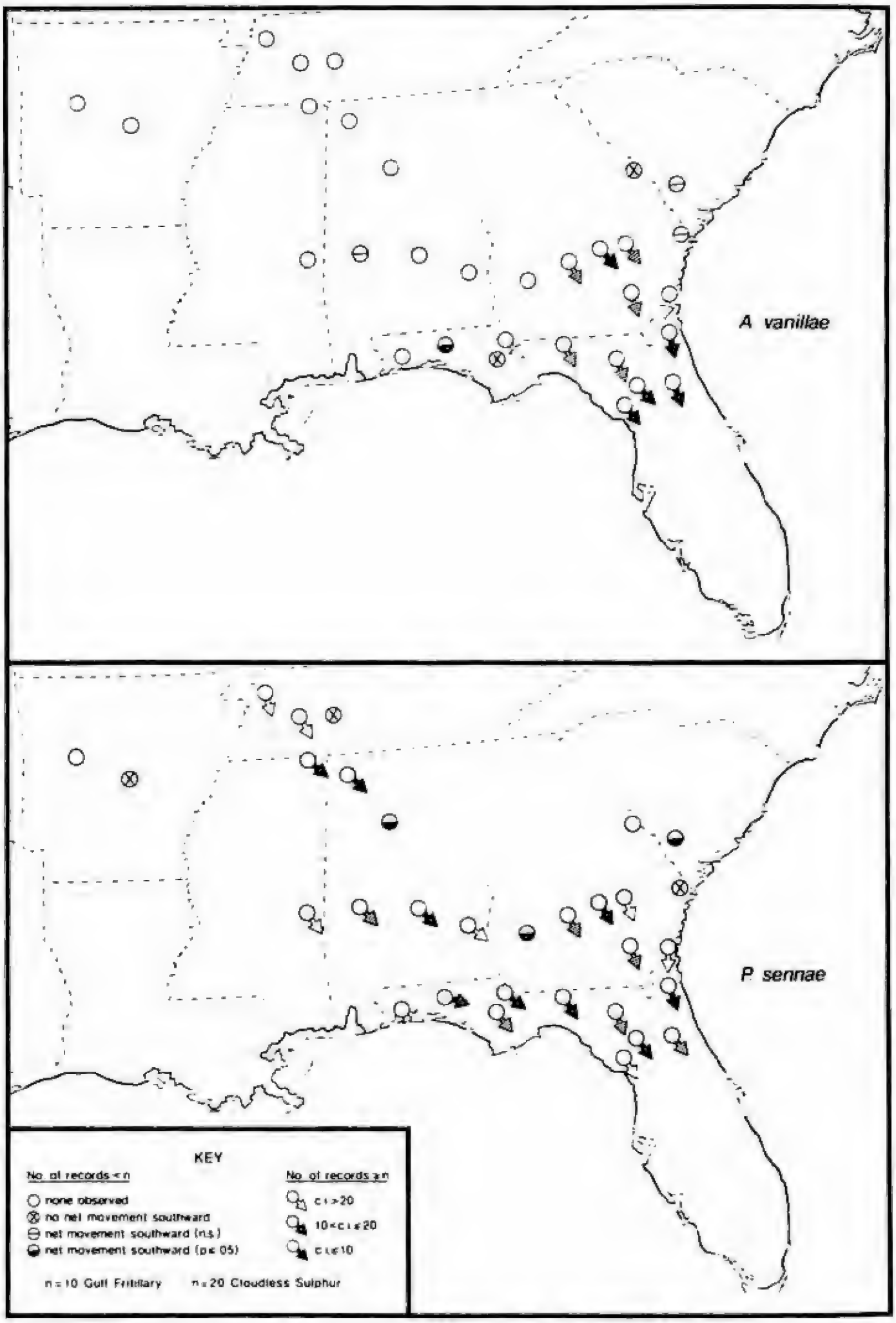

Figure 11

Summary of mean directions of *A. vanillae* and *P. sennae* during fall migration, 1982–83. (See Appendix 2 for detailed data.)

Monarch butterflies *(Danaus plexippus)* in eastern North America have the same sort of task as ***P. sennae***, ***A. vanillae*** and ***U. proteus***—i.e., to reach a common overwintering area from widely separated summer breeding areas. Their migratory flights differ from the ones described here in destination (central Mexico) and character (soaring flight at high altitude is common: Gibo and Pallett 1979, Gibo 1981, Brower, Schmidt-Koenig, this volume). Schmidt-Koenig (1979, this volume) studied directions of ***D. plexippus*** in their fall flights and reported significantly different directions at Ithaca, New York, and Blue Ridge, North Carolina. The directions, 224° and 215°, do not point toward a common destination, but Schmidt-Koenig (this volume) noted that they are in close agreement with a magnetoclinic model of pathfindng.

NUMBERS OF MIGRANTS

Methods

Numbers of migrants flying southward through north peninsular Florida were estimated by two independent methods. The first used polyester flight traps (see Walker 1980, Walker and Riordan 1981). The second method, effected in fall 1983, depended on counting migrants as they flew between 3-m PVC poles at the GVL site. Every Monday, Wednesday and Friday, 31 Aug to 11 Nov, at 1130 and 1230 LMT, 15-min counts were made of ***P. sennae*** and ***A. vanillae*** that flew over a 45-m ENE-WSW line and of ***U. proteus*** that crossed the first 15-m of the line. Each 15-min count consisted of three 5-min periods separated by 1-min intervals. Butterflies that flew northward over the line were subtracted from those that flew southward.

Converting 15-min counts to estimates of total migration for a day required knowing how relative density of migrants varied as a function of time of day. This was studied by taking 15-min counts every 30 minutes during each of four days (Fig 8). These data indicated that 2.6% (***U. proteus***) to 8.0% (***A. vanillae***) of total migrants for a day flew during the 15-min periods beginning at 1130 and 1230 LMT. Because counts were made 3 of every 7 days during the migratory season, the counts were further adjusted by a factor of 2.33.

Results

Results of the two procedures are compared in Table 2. Estimates for ***P. sennae*** and ***A. vanillae*** are surprisingly consistent. ***U. proteus*** numbers show greater changes, but the values confirm visual impressions: in 1975 ***U. proteus*** seemed exceptionally abundant; in 1978 ***U. proteus*** seemed exceptionally rare.

The estimates in Table 2 are for net movement southward across an ENE-WSW line at Gainesville. For example, in fall 1983, 2,345,000 more ***U. proteus*** were estimated to have flown southward across each km of ENE-WSW line than flew northward. Total migration through north peninsular Florida depends on the ENE-WSW limits of migratory flights and the average density of net movement between

Table 2
Estimates of absolute numbers of fall migrants (1000's per km^2), Gainesville, Florida.

	Phoebis sennae	*Agraulis vanillae*	*Urbanus proteus*
Polyester traps[a]			
"1975"[b]	368	126	3956
1978[c]	480 ± 112	159 ± 75	406 ± 148
15-min counts[d]			
1983	292	113	2345

[a] 2 or 4, 6-meter flight traps; trapping efficiency estimated to be 10%

[b] 18 Sept to 26 Nov 1975, 26 Aug to 17 Sept 1976; 2 traps

[c] 29 Aug to 12 Nov 1978; 4 traps (mean estimate and 95% c.i.)

[d] Migrants counted 6 times weekly (MWF, at 1130 and 1230 h LMT) as they flew over a 45-m (*P. sennae, A. vanillae*) or 15-m (*U. proteus*) line, 31 Aug to 11 Nov 1983. Proportion of daily flight occurring during two 15-min counts estimated to be 0.050 for *P. sennae*, 0.080 for *A. vanillae* and 0.026 for *U. proteus* (Fig 8).

these limits. Fall migration occurs at least from Otter Creek to Palatka (Fig 10: OTC, PLK) an ENE-WSW distance of ca. 106 km. The only estimates of migration density are at GVL. Taking the ENE-WSW limits to be 100 km and the average density of net movement to be the same as at GVL, one can estimate total net movement of butterflies southward during a fall, in millions, by moving the decimals in Table 2 one place to the left—e.g., 234 million *U. proteus* in 1983. Other estimates range from 11 million *A. vanillae* in 1983 to 396 million *U. proteus* in 1975.

Discussion

The similarity of estimates made by independent methods suggests that estimates of migration density at GVL are correct within a power of 10. Estimates of total migration through north peninsular Florida, made by extrapolating the GVL results approximately 50 km toward both the Gulf and the Atlantic, are likely to be more inaccurate. To improve estimates of total fall migration, estimates of migratory density (absolute or relative to GVL) should be made at intervals across north peninsular Florida.

UNANSWERED QUESTIONS

While these studies clarified certain features of the fall migrations of *P. sennae*, *A. vanillae* and *U. proteus*, they highlighted four unanswered questions.

How do migrants orient?

That *P. sennae*, *A. vanillae* and *U. proteus* can maintain a compass direction is evident. How they do it is not. The two most orthodox possibilities are that they employ a time-compensated sun compass or a magnetic compass. The fact that fall migrants maintain their migratory direction on overcast days (though few fly) weakens but does not eliminate the sun compass hypothesis (Verheijen 1978). The fact that neither *P. sennae* nor *A. vanillae* have detectable biomagnetism weakens but does not eliminate the magnetic compass hypothesis (Jungreis 1982, Schmidt-Koenig, personal communication).

Do migrants navigate?

Figure 11 suggests that migrant *P. sennae* have a map as well as a compass—i.e., that they navigate as well as orient. Alternatives to a navigational hypothesis are (1) the pattern of *P. sennae* migratory directions is fortuitous, (2) the pattern reflects migrants orienting by the sun with the eastward component of their movements causing their clocks to lag behind sun time, sending them more southward, and (3) migrants are genetically programmed to fly along particular axes (thus the descendents of those that fly NW in the spring fly SE in the fall, etc.). The lagging-clock hypothesis assumes that migrants use time-compensated sun orientation (unproved) and that most south Georgia and north peninsular Florida migrants have recently come from the northwest. The genetic-program hypothesis becomes hard to defend if migrants from diverse sources interbreed in south Florida during the winter (unknown).

The geographical area most important for testing the navigational hypothesis is eastern Virginia and North Carolina. Here migrants should fly SW prior to turning S and SSE into Florida. An attempt to measure directions in that region in late Sept 1983 was canceled upon finding no migrants at Augusta, Georgia, and very few at Hampton, South Carolina (Fig 10; AUG, HPT). The literature records from inland in this area are anecdotal but do not support the navigational hypothesis (Fig 9; Shannon 1916; Clark and Clark 1951).

What is the origin of GVL migrants?

This question emphasizes that no direct evidence exists as to how far individual *P. sennae*, *A. vanillae* or *U. proteus* fly. Circumstantial evidence suggests that some individuals which fly through Gainesville have come from as far away as Kansas or Missouri. If a migrant maintained a speed of 5 $m \cdot sec^{-1}$ for 5 hours each day, it could fly from Columbia, Missouri, to Gainesville, Florida, in 15 days (1350 km at 90 $km \cdot day^{-1}$). During their fall migration, monarchs fly more than twice that distance (Urquhart and Urquhart 1978).

What is the destination of GVL migrants?

I have made no observations of fall migrations in peninsular Florida south of Gainesville and know of no records for *P. sennae*, *A. vanillae* or *U. proteus* except for *A. vanillae* and *U. proteus* flying southward along the coast at Indialantic (about 175 km down the peninsula from GVL) (Williams 1958, p. 41).

If tens, or hundreds, of millions of migrants pass through north peninsular Florida each fall (Table 2 and text), what becomes of them? These numbers compare favorably with numbers of monarchs at overwintering sites in Mexico (Brower 1977), yet no one has reported spectacular aggregations of butterflies in (well-explored) south Florida. Two facts are worth noting: south Florida is large enough to hold millions of nonaggregated butterflies without their making a spectacle, and *U. proteus*, the most numerous migrant, is individually inconspicuous. To illustrate the former fact, 400 million *U. proteus* distributed evenly over the four southernmost Florida counties (Dade, Monroe, Collier, Broward) would amount to 1 *U. proteus* per 408 m^2 (or 13 per American football playing field).

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APPENDICES

Appendix 1. Hours, times, and winds for successive locations of migration [illegible] during fall of 1963 and 1963. See Fig. 10 for location of sites. Different sites (i.e., Florida) in the same general locality are designated by numbers after the locality code (e.g., JUN-1, JUN-2).

Site	Date of observations	Elevation (MST)	Local Wind dir.	mph	No. of records (+1h, 1=1, 1-1h)		
[illegible]	11 Aug 63	1330-1430	[illegible]	1	18	9	1
	13 Aug 63	0737-1343	N	4	35	11	9
[illegible]	25 Aug 63	1230-1513	S	1	48	34	1
[illegible]	31 Aug 63	0915-1303	W	5	9	1	1
[illegible]-1	20 Aug 63	1223-1345	[illegible]	4	12	1	1
-2	1 Oct 63	1218-1331	[illegible]	8	16	8	13
-3	1 Oct 63	1348-1500	[illegible]	8	15	8	2
[illegible]	7 Oct 63	0823-1018	[illegible]	6	48	13	6
[illegible]	26 Aug 63	0909-1230	W	1	36	3	6
[illegible]	1 Aug 63	1333-1534	[illegible]	3	3	1	6
	17 Aug 63	1208-1343	W	3	37	9	6
[illegible]	25 Aug 63	1433-1521	[illegible]	4	17	6	6
	13 Aug 63	1413-1819	NE	1	15	6	1
	9 Oct 63	0933-1321	NE	2	7	4	5
[illegible]	2 Aug 63	0930-1032	NW	2	6	6	6
	3 Aug 63	0937-1834	W	3	26	6	6
	14 Aug 63	0913-0957	W	4	13	6	6
[illegible]	18 Aug 63	0800-1047	W	1	25	9	1
[illegible]	4 Aug 63	1134-1334	NW	1	1	0	0
[illegible]	14 Aug 63	1130-1334	[illegible]	0	13	1	6
[illegible]*	1 Oct 63	0900-1305	NE	2	78	25	100
	11 Oct 63	0930-1343	NE	1	47	7	46
	13 Oct 63	0934-1329	W	3	11	6	18
	5 Oct 63	0856-1720	NE	3	32	16	83
	6 Oct 63	0934-1730	NE	1	65	20	30
	7 Oct 63	1010-1531	[illegible]	9	183	47	133
[illegible]	14 Aug 63	1340-1371	W	3	7	4	3
[illegible]-1	16 Oct 63	0834-1130	NW	2	78	36	73
-1	9 Aug 63	0933-1042	[illegible]	6	4	9	6
-2	1 Oct 63	0933-1830	W	2	16	5	15
-2	2 Oct 63	1144-1230	[illegible]	8	53	6	4
[illegible]	13 Aug 63	1134-1334	NE	2	38	6	6
[illegible]	14 Aug 63	1340-1340	NW	3	11	6	6
[illegible]	14 Aug 63	1035-1140	W	1	18	3	5
	15 Aug 63	1313-1401	-	0	3	1	3
	23 Aug 63	0833-1328	W	1	12	9	6
	8 Oct 63	1013-1303	NW	0	1	6	6
[illegible]	1 Aug 63	1341-1301	W	1	12	7	8
[illegible]-1	13 Aug 63	1334-1327	NE	2	14	4	6
-1	15 Aug 63	0747-1245	NE	6	18	13	1
[illegible]	15 Aug 63	1137-1343	NW	2	46	8	1
	15 Aug 63	1027-1042	NW	0	1	0	1
[illegible]	14 Aug 63	0834-1130	W	1	34	6	6
[illegible]	14 Aug 63	1231-1313	W	1	30	2	10
	15 Aug 63	1334-1301	-	0	3	0	1
	23 Aug 63	1340-1357	W	1	34	14	6
[illegible]	6 Aug 63	1100-1340	W	1	13	8	6
	16 Aug 63	1433-1333	NW	1	19	9	1
[illegible]	4 Aug 63	0900-1300	-	0	0	0	0
[illegible]	7 Oct 63	1319-1335	NW	1	36	34	4
[illegible]	1 Oct 63	1417-1434	W	1	4	0	0
	5 Oct 63	1239-1438	[illegible]	0	21	14	23
[illegible]	8 Aug 63	1329-1347	W	1	2	0	0
	19 Aug 63	1333-1299	NW	2	1	0	0
[illegible]	25 Aug 63	1137-1342	NW	1	44	0	1
	13 Aug 63	1427-1442	[illegible]	0	1	0	1
[illegible]	14 Aug 63	0834-0953	W	1	30	0	0
[illegible]	14 Aug 63	1231-1313	W	1	30	2	10
	15 Aug 63	1334-1301	-	0	3	0	1
	23 Aug 63	1340-1357	W	1	35	14	6
[illegible]	6 Aug 63	1100-1140	W	1	22	8	6
	16 Aug 63	1432-1432	NW	1	19	9	1
[illegible]	4 Aug 63	0900-1300	-	0	0	0	0
[illegible]	7 Oct 63	1319-1335	NW	1	36	34	4
[illegible]	1 Oct 63	1417-1434	W	1	4	0	0
	5 Oct 63	1239-1438	[illegible]	0	21	14	23
[illegible]	8 Aug 63	1329-1347	W	1	2	0	0
	19 Aug 63	1333-1299	NW	2	1	0	0
[illegible]	7 Aug 63	1335-1305	NW	2	9	1	0
	26 Aug 63	0843-1431	NW	2	3	3	6
[illegible]	16 Aug 63	1430-1335	[illegible]	0	88	8	1
	15 Aug 63	1334-1334	-	0	30	12	5
	9 Oct 63	1406-1434	NW	1	18	6	3
[illegible]	1 Aug 63	1310-1431	W	1	7	0	0
	17 Aug 63	1044-1130	W	1	11	3	7
[illegible]	1 Aug 63	1130-1331	-	0	3	0	0

*Some [illegible] more dances in 1963 (1331 additional records) were omitted.

Appendix 2. Details for migratory directions shown in Fig. 11 and comparable data for D. pennata. (See Appendix 1 for year, LAT, wind direction and speed for observations at each site and date.)

Site (Date)	n	Rayleigh scatter: mean dir. r, 95% c.l.	n	Unimodal scatter: mean dir. r, 95% c.l.	n	Bimodal scatter: mean dir. r, 95% c.l.
[illegible] (11 Aug)	18 .57	131±24				
(13 Aug)	35 .93	140±7	11 .89	134±9		
all	51 .88	134±10				
[illegible] (13 Aug)	48 .98	132±4	34 .97	142±4		
[illegible] (26 Aug)	12 .97	140±8	1		4 .94	149±14
(1 Oct)	16 .88	148±20	8 .88	148±20	12 .88	136±8
(5 Oct)	25 .95	138±4	6 .79	138±8	1	
all	41 .89	142±7	14 .93	144±10	16 .94	136±8
[illegible] (1 Oct)	49 .79	138±11	13 .91	147±13		
[illegible] (26 Aug)	36 .94	148±7				
[illegible] (1 Aug)	5 .99	138				
(17 Aug)	57 .98	133±4				
all	62 .96	133±3				
[illegible] (25 Aug)	17 .79	134±12				
(13 Aug)	51 .87	97±8				
(9 Oct)	7 .98	148				
all	75 .74	121±11				
[illegible] (1 Aug)	6 .98	138±13				
(5 Aug)	36 .76	134±13				
(16 Aug)	15 .92	178±25				
all	45 .73	136±14				
[illegible] (19 Aug)	39 .83	134±13				
[illegible] (16 Aug)	31 .93	139±8				
[illegible] (1 Oct)	79 .88	147±6	25 .97	138±6	136 .94	143±3
(11 Oct)	47 .85	154±9	7 .85	121	46 .88	148±8
(13 Oct)	31 .91	137±9	6 .92	128	26 .90	149±10
(3 Oct)	12 .74	140±16	10 .88	128±14	83 .95	140±3
(4 Oct)	65 .85	141±11	29 .97	127±11	99 .96	142±4
(7 Oct)	183 .66	141±10	45 .87	146±8	153 .96	141±3
all	358 .77	140±4	136 .88	136±4	496 .93	142±1
[illegible] (10 Oct)	79 .88	153±5	36 .96	139±5	73 .91	173±3
(6 Sept)	7 .99	187				
(1 Oct)	24 .93	173±10	4 .94	178	12 .61	131±26
(2 Oct)	47 .95	177±5	6 .98	168	9 .66	156±38
all	157 .97	163±4	47 .98	170±4	93 .83	166±8
[illegible] (14 Aug)	30 .75	153±14				
[illegible] (24 Aug)	13 .72	153±13	1		5 .99	148
(21 Aug)	3		1		2	
(25 Aug)	33 .93	147±8	9 .96	143±13	6 .73	153±30
(8 Oct)	1		6 .95	154	6	
all	54 .88	151±9	19 .94	148±9	19 .91	151±20
[illegible] (11 Aug)	32 .72	139±13	1			
(23 Aug)	14 .96	134±8	9 .99	144±14		
(25 Aug)	18 .98	171±16	11 .98	148±14		
all	38 .85	144±13	21 .98	147±9		
[illegible] (26 Aug)	46 .92	134±12				
(13 Aug)	1					
	47 .92	135±13				
[illegible] (14 Aug)	30 .98	147±14				
[illegible] (14 Aug)	30 .94	136±6	3		14 .97	140±4
(21 Aug)	2		4		1	
(22 Aug)	35 .97	141±4	16 .98	139±7	6 .94	131
all	65 .92	140±5	19 .98	134±7	21 .97	147±4
[illegible] (4 Aug)	32 .94	134±6				
(14 Aug)	19 .98	142±4				
(all)	51 .96	138±5				
[illegible] (7 Oct)	36 .73	131±13	34 .97	143±4		
[illegible] (2 Oct)	4 .98	134			6 .98	134±13
(5 Oct)	15 .93	137±8	14 .98	139±3	13 .91	131±10
all	19 .95	135±7	14 .99	139±3	19 .98	147±5
[illegible] (16 Aug)	49 .98	132±2	6 .97	138±16		
(13 Aug)	44 .93	135±5	12 .88	131±18		
(9 Oct)	13 .88	144±14	6 1.00	131		
(all)	94 .98	133±4	24 .98	136±11		
[illegible] (1 Aug)	7 .98	134				
(17 Aug)	31 .95	134±5				
all	38 .94	134±4				

ECOLOGICAL FACTORS WHICH INFLUENCE MIGRATORY BEHAVIOR IN TWO BUTTERFLIES OF THE SEMI-ARID SHRUBLANDS OF SOUTH TEXAS

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ABSTRACT

Temporal and spatial patterns of drought and rainfall influence patterns of host leaf production and extent of parasitoid-induced mortality in south Texas Lepidoptera. These factors can in turn interact to induce population outbreak and migratory flight in ***Libytheana*** and ***Kricogonia***, two butterflies which depend upon new growth of the shrubs ***Celtis*** and ***Porlieria*** respectively. Differences between these shrubs in seasonal phenology and resistance to, or response to, defoliation result in asynchronous migratory flights and different degrees of sexual dimorphism for onset of migratory flight by the two insects. Adults of both butterfly species may respond to declining resources by entering reproductive diapause locally, or by initiating migratory flight. However, details of such responses vary with species and time of year and remain a fertile direction for future research.

INTRODUCTION

Like many natives of south Texas, I have, since childhood, been fascinated by periodic and often massive migrations of two butterfly species: the pierid ***Kricogonia lyside*** (Fig 1A) and the snout butterfly, ***Libytheana bachmanii*** (Fig 1B). From 1965–1980 and especially from 1976–1980, I made sporadic observations sufficient to discern certain patterns in the migratory behaviors of these species and to develop hypotheses concerning the ecological causes of such patterns.

Figure 1

Two migratory butterflies of southern Texas. A. (above) shows a diapausing *Kricogonia* along Sage Creek, June 1977. B. (below) is a snout butterfly, *Libytheana*, also at Chaparral Wildlife Management Area, July 1976.

Area and Climate

Observations were carried out near Catarina, and 19 km east on the 6,154 ha Chaparral Wildlife Management Area, Dimmitt County, Texas. The study area, like much of southern Texas, is a shrubby grassland dominated by mesquite and prickly pear (Whittaker et al. 1979).

The climate is semi-arid and prone to drought. Rainfall averages about 49 cm per year, with midsummer tending to be the driest period. But in the highly unpredictable climate that characterizes the Rio Grande Plain of Texas, average conditions bear little relationship to the actual conditions faced by organisms in their lifetimes. In addition to such temporal heterogeneity, spatial patchiness in rainfall is

another major feature of the midsummer environment of south Texas which greatly influences the evolution of life history tactics of mobile organisms native there. Stations only 16 km apart may differ by 15–25 cm in July rainfall.

Such spatial and temporal uncertainties, while they select for interesting diapause and migratory tactics, make study difficult. I have been fortunate to have observed and recorded events which may not be repeated during my lifetime on those few areas to which I have access. One goal of this paper is to help focus attention on aspects of this system that present questions of general interest which are also accessible to short term experimental analysis.

Organisms

Kricogonia has been cited as a migrant since the 1940's but only in brief notes by field collectors. ***Libytheana bachmanii***, by contrast, has been generally recognized as a migrant from much earlier, and ***Libytheana*** species are well-known migrants in Africa and Asia (see for example, Williams 1930, 1958).

Hostplants of the two insects, ***Porlieria augustifolia*** for ***Kricogonia***, and ***Celtis pallida*** for ***Libytheana***, are components of shrub clumps which develop around nitrogen-fixing mesquite (Gilbert, in press), and are common in native rangeland of south Texas. Both butterflies restrict oviposition to very new growth of hosts since young larvae can develop only on tender leaves. It appears that the different timing of migrations of the two species relates to phenological differences in new leaf production by the two shrubs, and synchronized migrations of the two species (e.g., Clench 1965) are exceptional.

KRICOGONIA LYSIDE

Kricogonia lyside (Godart) is characterized by spring migrations, female reproductive diapause, and female-biased sex-ratio in migratory populations.

Porlieria (Zygophyllaceae), the hostplant used by ***Kricogonia***, is a bonsai-like shrub with thick, succulent stems having sparse foliage of pinnately compound leaves. ***Porlieria*** flushes new leaves and flowers each spring, even in drought years (personal observation).

By March following a mild winter, overwintering female ***Kricogonia*** can deposit eggs singly on new leaves of ***Porlieria***. Young larvae only grow on new leaves and even last instar larvae prefer, if not require, relatively new foliage. Mature leaves seem highly resistant to ***Kricogonia*** attack: I have not observed total defoliation of a plant by ***Kricognia*** larvae. After harsh winters, ***Kricogonia*** must recolonize by dispersal from northeast Mexico.

Once ***Porlieria*** new growth is consumed, there is typically a delay before further new growth appears on the plant. Eggs are not placed on plants which lack new shoots even though they may be frequently investigated by mated females. Delay in leafing out after defoliation is one aspect of ***Porlieria*** phenology which sets it apart from ***Celtis*** and must account for some of the differences in diapause and migration

tactics evolved by ***Kricogonia*** and ***Libytheana*** respectively.

In the case of ***Kricogonia***, migratory flights often involve movement of both sexes from areas temporarily devoid of new growth (because of their own larval feeding) to areas ***likely*** to have new growth available. During most years in southern Texas, moisture and vegetative conditions suitable for ***Kricogonia*** breeding and development prevail during the spring, and migrations are most often seen from mid-April through late May (Table 1).

Mid-May appears to represent an important switch point for ***Kricogonia*** reproductive tactics. After that point, deterioration of local conditions (i.e., loss of suitable larval and adult resources) results in sedentary behavior and female diapause. This pattern makes sense in view of long term averages for early summer conditions which face the next brood: this is the period during which the likelihood of rain declines to a yearly low for the area. Dispersal during late May into July from local patches in decline is likely to be futile. Thus from June to July it should be better for individual ***Kricogonia*** to wait for improvement of the patch in which they originated or to delay migration at least until chances of finding suitable patches improve. I studied a diapausing population along Sage Creek at Chaparral WMA in June 1977. I believe the following account of that population is a reasonable first approximation of diapause biology for this species.

Conditions were favorable for the production of large adult populations of ***Kricogonia*** in spring 1977 (large overwintering population of 1976−1977 which could effectively utilize the March pulse of new growth). By late May and June, conditions were rapidly deteriorating in what would become a severe drought (June 1977−May 1978). Rather than move, adults retreated to shaded corridors along dry drainages such as Sage Creek. By dissection, I determined that females were in reproductive diapause (Table 2) but males, for the most part, were sexually active. Both sexes spent most of their time perched near the ground, under leaves, along shaded dry gullies and creeks. Roosting sites were 5°C cooler than exposed sites nearby (34°C vs. 39°C).

Males spent much of the day involved with precourtship chases which usually only involved other males. These males would frequent any suitable nectar sources (e.g., ***Monardia***).

Most females sampled from the diapausing population, had mated at least once. I dissected 20 females and found that 16 of 17 fresh (young) individuals contained immature eggs and abundant fat body, but only 3/17 were virgin. Only older individuals, presumably from a previous generation, possessed mature eggs and multiple (2−3) spermatophores (see Table 2). In studying these diapausing females, I noted a satellite of the bursa copulatrix (Fig 2) which varied in size and appearance with female reproductive status. Its size ranged from 0.7 mm in two unmated females to 1.3 mm in a female bearing mature eggs and three spermatophores. It was translucent and empty in virgins, but in mated females the structure contained a yellow fluid which turned white in 95% ethyl alcohol. Other pierids possess this structure and its possible role in diapause storage of sperm should be investigated.

Table 1

Summary of migration, diapause, and reproductive activity observed for *Kricogonia* in central and south Texas 1883–1980. Letters N,S,E, and W designate approximate month and direction of noted migration along year rows. Δ indicates notable rain immediately preceeding migratory movement, box (□) indicates sedentary populations in reproductive diapause, R indicates reproductive activity (courtship plus egg laying), and minus (–) indicates that no *Kricogonia* were found in spite of thorough search. Stipled parts of table highlight periods with no recorded migrations. Sources are as follows: A = Aaron (1882), B = Lacey (Kendall and Kendall 1971), C = Sweetman (1940), D = Wilson (1949), E = Kendall (unpublished field notes), F = Clench (1965), G = Gilbert (unpublished field notes), H = Davis (unpublished field notes).

Source & Year	March	April	May	June	July	August	Sept	Oct	Nov
A 1883					N				
B 1902		S							
B 1918			E						
C 1939			ΔSE						
D 1948									
E 1956					SW				
F 1963					N				
G 1965				□[1]					
E 1967		ESE							
G 1970				R[1]					
G 1973					ΔR[1]				
G 1976				ΔR[2]					
G 1977				□ΔR[2]		–[2]			–[2]
E 1977		WNW							
G 1978		□(?)	ΔN[2]			□[2]			
H 1978			ΔESE[2]						
E 1978					ΔNE				
H 1979		□ΔSE[2]							
G 1979			□/R[2]						
G 1980			ΔSE[2]						

[1] = entries from Chaparral Wildlife Management Area

[2] = entries from Catarina. See text for discussion.

Moderate rainfall (2.7 cm) on 12 June 1977, just prior to my observation period (16–30 June) brought out new growth on a few *Porlieria* near Sage Creek. Coincident with this change in the status of hostplant, a few females were seen to investigate oviposition sites about 800 m from the diapause area. These females were actively courted by males, and one of two dissected females contained a second, fresh spermatophore, indicative of recent mating. In the diapause area at this time one

Table 2

Reproductive status (left column) of females caught along Sage Creek, 16–26 June 1977. Individuals of intermediate condition (i.e., older) are indicated by asterisks. Of 20 females, 15 or 75% possessed 1 spermatophore; of these only one (1/15) carried mature eggs.

	Number of Spermatophores				
	0	1	2	3	Total
Small Oocytes (0.1–0.3mm), No Vitellogenesis	3	8	0	0	11
Developing Oocytes (0.4–0.7mm) Some Vitellogenesis	0	6	0	0	6
Mature Eggs (0.9mm)	0	1	1*	1*	3
Total	3	15	1	1	20

could observe a few females leaving to visit nearby hostplants, but the majority remained in place. Thus in spite of an average state of diapause, a few individuals, because of age, differential experience, or genetic disposition, appeared to possess different thresholds and/or criteria for breaking diapause. By 30 June 1977, many adults were actively reproducing away from the diapause area. Extensive larval damage on *Porlieria* new growth was evident, but the fate of these larvae is unknown. The area did not receive substantial rain for another year. No *Kricogonia* were found along Sage Creek or elsewhere on Chaparral WMA when I visited the area five months later on 24 November 1977.

Why only a fraction of the Sage Creek population broke diapause in late June 1977 is not certain. Another pattern worth further study is microsite variation in diapause state. During 10–11 May 1979, all female *Kricogonia* seen at Sage Creek appeared to be in diapause. Two miles away along another drainage, ovipositing females were very abundant and no conspicuous diapause population was evident, nor was migratory activity observed.

Even more dramatic differences can be seen during a given month at the same site between years. In contrast to the large diapause population seen in May 1979, *Kricogonia* were virtually absent at Sage Creek, except for individuals moving through the immediate area on migration 26–27 May 1980. Heavy migrations were also seen in May 1978. These and other observations are summarized in Table 1.

Figure 2

Field-dissected bursa copulatrix and ovaries of *Kricogonia* female. The bursa satellite varied from 0.7 mm in virgins, to 1.0 mm in once-mated females as shown and 1.3 mm in multiply mated females. Chaparral WMA, June 1977. Scale = 1.7 mm.

Kricogonia migration should occur under two distinct circumstances. First, as in the case of ***Libytheana*** (see below), migration may immediately follow defoliation of the hostplant's new growth. Second, migration may occur after diapausing populations experience improved conditions such as rainfall and the appearance of new growth on ***Porlieria***.

The first category (Type I) of migration is hypothetical for ***Kricogonia***. Such migrations, lacking a prior sedentary phase of reproductive diapause, should only occur in broods emerging from April through early May and possibly from mid-July to mid-September. These are the intervals during which rainfall probabilities are increasing on the Rio Grande Plain (see Fig 7), i.e., when dispersing individuals are likely to find suitable patches (nectar and oviposition sites) for reproduction somewhere in the region.

Migrations of ***Kricogonia*** (ESE) were observed on 21 April 1979, by Paul Davis. Later that spring, 10 May 1979, I dissected individuals (assumed to be part of the same population) perching along Sage Creek and found them to be in diapause. Thus it appears that Type I migration may end with individuals becoming sedentary and remaining in diapause if suitable habitats and/or conditions are not encountered, or

if they are seeking diapause sites.

The second category of migration (Type II) exhibited by *Kricogonia* is less hypothetical. It occurs when diapausing individuals terminate their sedentary phase and move to new areas where reproductive activities take place. The evidence for Type II migration is the fact that migrations can be initiated within a few days of rains terminating drought. Sweetman's (1940) report of 30 May 1939 (SE) migrations near Uvalde, TX, and Paul Davis' (personal communication) report of 29 May 1978 (ESE) migration near Sage Creek have in common the fact that the lag between the onset of rain (two days in 1939; 11 days in 1978) and the observed migrations was well short of *Kricogonia*'s generation time. In other words, migrating individuals must have been adults waiting for conditions to change. See other examples in Table 1.

One difference to expect between Type I and Type II migration is the degree of female bias in the sex ratio of migrating groups. For Type I migrations, the sex ratio of migrating individuals should increasingly reflect the primary sex ratio as the migration proceeds. For Type II migrations, heavy female bias should be observed with predominance of females increasing as the preceding diapause period lengthens. This prediction results from the fact that females, not males, diapause and the resulting likelihood that males have much shorter life expectancies. All (25/25) of migrating individuals caught by Davis at Chaparral on 29 May 1978 were female. On the other hand, under conditions for Type I migration, females are predicted to leave first in response to declining oviposition cues, males slightly later as females become more difficult to encounter. It should be noted that degree of protandry, unknown for *Kricogonia lyside*, will influence such predictions.

This account is based on sporadic, short term observations, with almost no careful observations in the August–October period. However, it is safe to say that *Kricogonia*, because of the facultative and diverse nature of its response to changing environments, provides a rich opportunity for the experimental study of the physiology, ecology and evolution of diapause and migration tactics in insects.

If cues which trigger diapause breaking and/or migration act directly on adults and are as sex specific as they seem to be, local manipulations such as irrigation of host patches or presentation of volatiles from host new growth should induce rapid and predictable changes during different times of the year (for example Carlisle, Ellis and Betts 1965). Likewise, careful studies of the dynamics of migrations, both at their origins and through time, will be necessary to verify the hypothesized Type I and Type II migrations and to fully understand differential responses of the two sexes. Alternative explanations for female-biased sex ratios in migrating populations such as so called sexual harrassment (Shapiro 1970) deserve consideration.

In spite of our sketchy knowledge of *Kricogonia*, it is clear that it provides a dramatic and informative contrast to the most conspicuous migratory insect of south Texas: the snout butterfly, *Libytheana bachmanii*.

LIBYTHEANA BACHMANII LARVATA

Libytheana bachmanii (Strecker) is characterized by late summer migration, region-wide movements, and male-biased sex ratio in migratory populations.

Spectacular migratory swarms of ***Libytheana***, up to 400 km wide, have been reported numerous times during this century by observers in south Texas. Most reports take the form of brief accounts in entomology journals and do little more than report direction of flight, dates, and recent weather conditions. Virtually none of the many reports document the sex of the migrants, nor is the phenomenon of snout butterfly migration discussed in the broader contexts of insect migration except by Williams (1930, 1958). Neck (1983), by comparing weather records with data on snout migration, was the first to make any sense out of known patterns of snout outbreak and migration: population size is positively correlated with the intensity and duration of dry periods immediately preceding drought-terminating rains.

Migrations of the snout butterfly may not be more frequent than those of ***Kricogonia***, but they have been more frequently reported in the literature possibly because the season for ***Kricogonia*** migration (April–May) ends before the summer field season for lepidopterists begins. Moreover, ***Libytheana*** host plants are more abundant and are more completely converted to adult butterfly than is the case with ***Kricogonia***. ***Libytheana*** migratory swarms are spectacular for their density, duration and geographical extent. In late September 1921 an estimated 25 million per minute southeasterly-bound snout butterflies passed over a 400 km front (San Marcos south to the Rio Grande River). Gable and Baker (1922) noted that this flight lasted 18 days. It may have involved more than 6 billion (6×10^9) butterflies.

The biotic interactions potentially relevant to ***Libytheana*** outbreak and migration are more varied and complex than those known for ***Kricogonia***. The desert hackberry ***Celtis pallida*** is one of the most common shrubs of south Texas. It is the primary host for ***Libytheana***, ***Asterocampa leilia***, and for ***A. celtis antonio***, two of several species of so-called hackberry butterflies. Sugar hackberry ***Celtis laevigata*** is the hostplant for ***Libytheana*** and ***Asterocampa*** in central Texas, and exists in semi-arid south Texas only along rivers, creeks, and drainage areas such as Sage Creek. A third hackberry butterfly species (***A. clyton texana***) at Chaparral WMA is found along narrow belts of more mesic vegetation (e.g., Sage Creek) to which its host *C. **laevigata*** is restricted.

A. clyton and ***L. bachmanii*** share at least one parasitoid, a chalcid (***Brachymeria***) ***sp.*** which develops in pupae and which occasionally acts as a major mortality factor for ***A. clyton***. For ***Libytheana***, ***Asterocampa*** is potentially a parasitoid reservoir maintaining a significant factor against population increase. In less arid zones, such as central Texas, ***Celtis***, ***Asterocampa***, and ***Libytheana*** are all present but ***Libytheana*** population explosions and migrations are extremely rare and only follow unusual drought as in September 1971 (Helfert 1972). The drought of 1977 that preceded the snout butterfly outbreaks and migrations at Chaparral in 1978, left many ***Celtis laevigata*** leafless or dead and ***Asterocampa clyton*** missing from the area where it is usually resident.

By contrast, one *Asterocampa* species that shares *Celtis pallida* with *Libytheana* was negatively affected by *Libytheana* outbreaks. In March 1977 and in May 1979, I found miniature *A. celtis* males (each 20 mm forewing length) in areas where the snout butterfly had defoliated their shared host the previous July (1976) or August (1978) presumably forcing *A. celtis* larvae to pupate well before maximum size was attained. During the same periods,, *A. clyton* were not unusually small as their host plant (*C. laevigata*) was not defoliated by snout larvae. A detailed knowledge of interactions in this system of insect and plant species will be needed before a full understanding of *Libytheana* outbreak and migration cycles is achieved.

A sample of snout butterfly migration records obtained in Texas south of Austin is presented in Table 3. Note that snout migratory activity begins just at the end of *Kricogonia*'s migratory season, i.e., late June–early July (Table 1). It is during this period when the rare joint flights have been observed (e.g., 4 July 1963, by Clench (1965) and 4 July 1956, by Kendall, personal communication). Like Kricogonia, snouts are not typically found migrating during the month of June. Since both species live in the same habitat, the fact that one tends to migrate early and and the other late in the season must ultimately relate to details of their respective life histories, especially their interactions with larval hostplants.

In most years, *Porlieria* and *Celtis pallida* are in the process of leafing out by mid-March at Chaparral WMA. However, *Celtis* seems less well-buffered against extreme dry conditions than does *Porlieria* since development of its new growth can be arrested by extreme drought (personal observation). Thus, regardless of climatic conditions, there is always a spring brood of *Kricogonia* emerging in April, assuming that a population of over-wintering adults is available. By contrast, early spring production of snout butterflies does not appear to be automatic even if adults are available. These differences do not clearly reveal why snout butterflies do not migrate in the spring, but suggest certain approaches to the question such as experimentally supplementing the adult snout population on artificially irrigated patches of *C. pallida* during April and May, simulating conditions that naturally lead to migrations later in the year (July–September) as will now be discussed.

During the summers of 1976, 1977 and 1978, I was able to observe an extreme range of weather conditions and associated migratory responses by snout butterflies. Because no other migrations have been studied at points of origin, my data on these events at Chaparral WMA are the first glimpses into the biology of migration for *L. bachmanii*. Because of the coincidence of unusual weather with my visit to the area, I was able to observe a full range of snout butterfly population events from localized outbreak and migration from drainage areas in July 1976, to low density and no migrations during the drought of 1977–1978, to region-wide outbreak and mass migrations of August 1978.

On 26 July 1976, while involved with a graduate field course at Chaparral WMA, several of my students discovered a narrow drainage zone in South Jay Pasture where snout butterfly larvae had totally defoliated the available *Celtis pallida* shrubs (I call the area "Snout Creek"). Although a few larvae were still in evidence, most individuals were pupae, 2027 and 400 of which were removed from a 3 m diameter

Table 3

Migratory and diapause activity of snout butterflies in south and south-central Texas 1912–1980. Month and year are indicated by column and row of flight direction entry (N,S,E,W). Migrations not having direction specified are indicated M. Diurnal reversals in flight direction are indicated by <. Large populations sitting around are assumed to be in reproductive diapause, □. Reproductive populations are denoted by R. Minus (–) indicates that no *Libytheana* were found in spite of thorough search. Notable rainfall is indicated by Δ. Stipled parts of table indicate periods with no recorded migration. Sources are as follows: I=Smyth (1920), J=Bernheim (1917), K=Parman (1926), L=Gable and Baker (1922), M=Rau (1941), N=Breland (1948), O=Helfert (1972), E=Kendall (unpublished field notes), F=Clench (1965), G=Gilbert (unpublished field notes).

Source & Year	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec
I 1912				E						
J 1916							N			
K 1916					Δ Δ	SEΔ ΔSE			–	–
K 1921					SE	SE SE				
L 1921						SE				
M 1940					E					
N 1947						W				
E 1956					SW					
F 1963					NE					
E 1963					P					
O 1971						NE				
E 1971					SE	SE<		NW<□		
E 1975						□	SE			
G 1976					SW	W<				
G 1977									□	
G 1978			– Δ	M	Δ	S				
E 1978					□ Δ	□ NE<				
G 1979			< –							
G 1980							R			

and a 1.5 m diameter bush respectively (see Figure 3). On 26 July, adult emergence had been underway approximately 1–2 days and a small trickle of migrating adults were heading southwest (230°) 8–13 km per hour at an angle to northwest (320°) 16–24 km per hour winds. The resultant west southwest flow crossed the Artesia Wells-Catarina highway (FM 133) 3 km away. This created a 5.6 km front of migrating snout butterflies which, at peak density on 28 July 1976, were passing a 15 m front at a rate of 25 per minute.

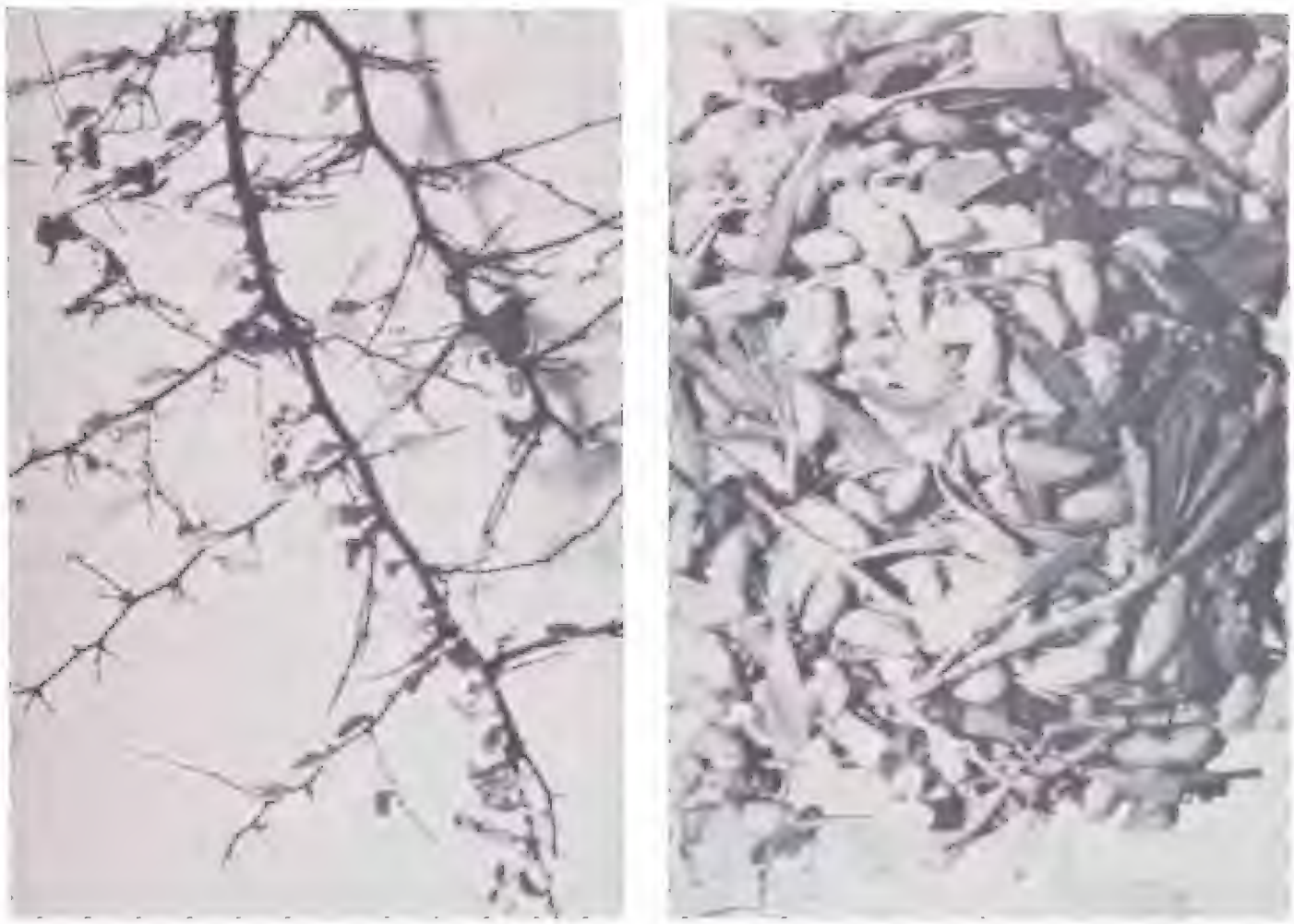

Figure 3

Pupae of *L. bachmanii* in the defoliation zone called "Snout Creek." A. (left) shows pupae and empty pupal cases on a defoliated *C. pallida* branch. B. (right) shows a fraction of 2027 pupae collected from a single bush.

What were the ecological circumstances of this migration? First, Chaparral WMA received 3 cm of rainfall between 16–20 June. I arrived on the first of two visits in 22 June to find that shrubs including *C. pallida* were already flushing new growth in response to these rains. Although all butterflies, including snouts, were uncommon at that time, eggs laid during the period had high quality host leaves and presumably low parasitoid levels as larvae. Under optimal conditions, the egg to adult period for *L. bachmanii* can be 16 days (R. Kendall, personal communication) so that the brood observed defoliating *C. pallida* and migrating in late July were quite likely the grand offspring of adults seen on 22–25 June.

Two generations were possible because of unusual rains in early to mid-July 1976. Chaparral WMA received 28 cm during that period (about 26 cm above normal for the month). Nineteen kilometers to the west in Catarina, July rains amounted to 18 cm, but June was dry and there were no snout migrations in July. I conclude from these observations that outbreaks involving defoliation and migratory movements require not only a strong pulse of new foliage when parasitoid pressure is probably low (e.g., at the end of a drought) but also the existence of a resident adult population or recent immigrants, capable of opportunistically exploiting the window of optimal

conditions. It follows that the spatial and temporal pattern of new growth availability and the size of prior adult populations are variables that should determine the magnitude of snout outbreak. This simple idea was well supported by the events of August 1978, as will be detailed later in this paper.

Other aspects of the 1976 migration deserve mention here. First, I asked how the two sexes might differ in timing of migration. I reasoned that if these insects, as adults, were responding to changing conditions on short notice, then the sexes might well differ, for example, in what constitutes optimal leaving time. The prediction was that newly emerged females should leave first because the defoliation would eliminate suitable oviposition sites. Conversely, I reasoned that males should wait since virgin females eclose each day at the site. Leaving to search elsewhere seemed risky. With this expectation, I set out with my class to collect sex ratio data from (1) pupae collected at the site, (2) adults feeding on nectar or drinking at mud near the site, (3) the migrating group crossing the highway early in the migration and (4) the same stream of butterflies later in the flight. Two related null hypotheses were, first, that in leaving time the sexes would not be different, and second, that if they were different, males would leave first. Observation rejected the first, but not the second, null hypothesis.

The sex ratio results are shown in Table 4. Since no previous reports of snout migrations had documented the sexes of sampled individuals, I had no warning as to how wrong my initial reasoning on the second hypothesis was. While the sex ratio of adults emerging from collected pupae was near unity, adults migrating the day those pupae eclosed were virtually all males, a sex ratio of 83.5. Only later in the migration did the females begin to join. On 11 August 1976 the sex ratio stood at 7.0 (see Table 4).

Further observation in the emergence zone revealed that rather than being devoid of oviposition sites, defoliated *C. **pallida*** was breaking new bud as if in spring. Females mated as they emerged and remained to lay eggs on these new shoots. A haphazard sample of 50 shoots revealed 27 eggs. Under typical conditions, 10 to 100 times that number of new shoots would be required to harvest 27 eggs of ***Libytheana*** at Chaparral WMA.

If females are staying home to reproduce, why were so many males leaving? I believe that newly eclosing males of the snout butterfly have similar problems to juveniles of many birds and mammals. They have little chance to mate in their natal area and disperse to seek better sexual opportunity elsewhere. A look at the progress of an emergence helps explain a male snout butterfly's dilemma. In the first few days of the emergence, older males from a previous brood very likely mate all of the newly eclosing females. Their brothers would be mature enough to compete for new females a few days later, at which time and progressively thereafter, each day's new males are facing increased competition from an accumulating pool of older males for a constant or decreasing daily pool of available virgins. At some point during the emergence, males will fare better if they fly off to compete for females in areas in which the timing of emergence is shifted later relative to their own site of origin.

Table 4
Sex ratio of snout butterflies in area of *Celtis* defoliation, South Jay Pasture ("Snout Creek"), Chaparral Wildlife Management Area, July–August 1976.

	Males	Females	Sex Ratio
Pupae on *Celtis* 27 July 1976	79	69	1.15
Adults on *Condalia* flowers 27 July 1976	26	14	1.86
Adults on Mud 27 July 1976	47	3	15.67
Adults Migrating 28 July 1976, 1100 hours 11 August 1976, 1130 hours	167 76	2 11	83.50 6.91

The requisite spatial and temporal heterogeneity of rainfall favoring the evolution of such tactics is a salient feature of south Texas during the summer months. A rancher may watch his neighbor receive heavy rains while his own pastures wither and blow away. Such patchiness in convectional thunderstorm activity can be detected in official weather records. In June 1965, Encinal received 0.0 cm, Cotulla 4.3 cm, Carrizo Springs 0.8 cm, and Catarina 0.0 cm of rainfall. In July 1959, the same stations received 1.8 cm, 1.9 cm, 7.3 cm, and 2.2 cm respectively. Flying at a speed of 8–13 km per hour, a snout butterfly could easily move between any two of these stations in less than one day (see Fig 4). For its hostplant, and thus for this insect, a difference of 5 cm rainfall from time to time or place to place is highly significant when the range is 0–5 cm!

Since the July 1976 migration appeared to be the local patch to patch type flight, I attempted to negate the null hypothesis, i.e., that it was a long range flight. On 31 July 1976 a minimum of 35 hours of prime flying time since our first sightings of the migration, my brother, Thomas Gilbert, a resident of Laredo, drove the public roads from Artesia Wells, past Chaparral and through the continuing flight (Fig 4) to Catarina and south to Hilltop. From there, he drove east to Encinal. No other migrations were encountered. The Snout Creek migrants, capable of traveling over 100 miles in the available time, had settled somewhere in the private ranch land circumscribed by Texas FM 133, Highway 83, FM 44, and IH 35. One possible destination is the San Rogue Creek drainage indicated in Figure 4.

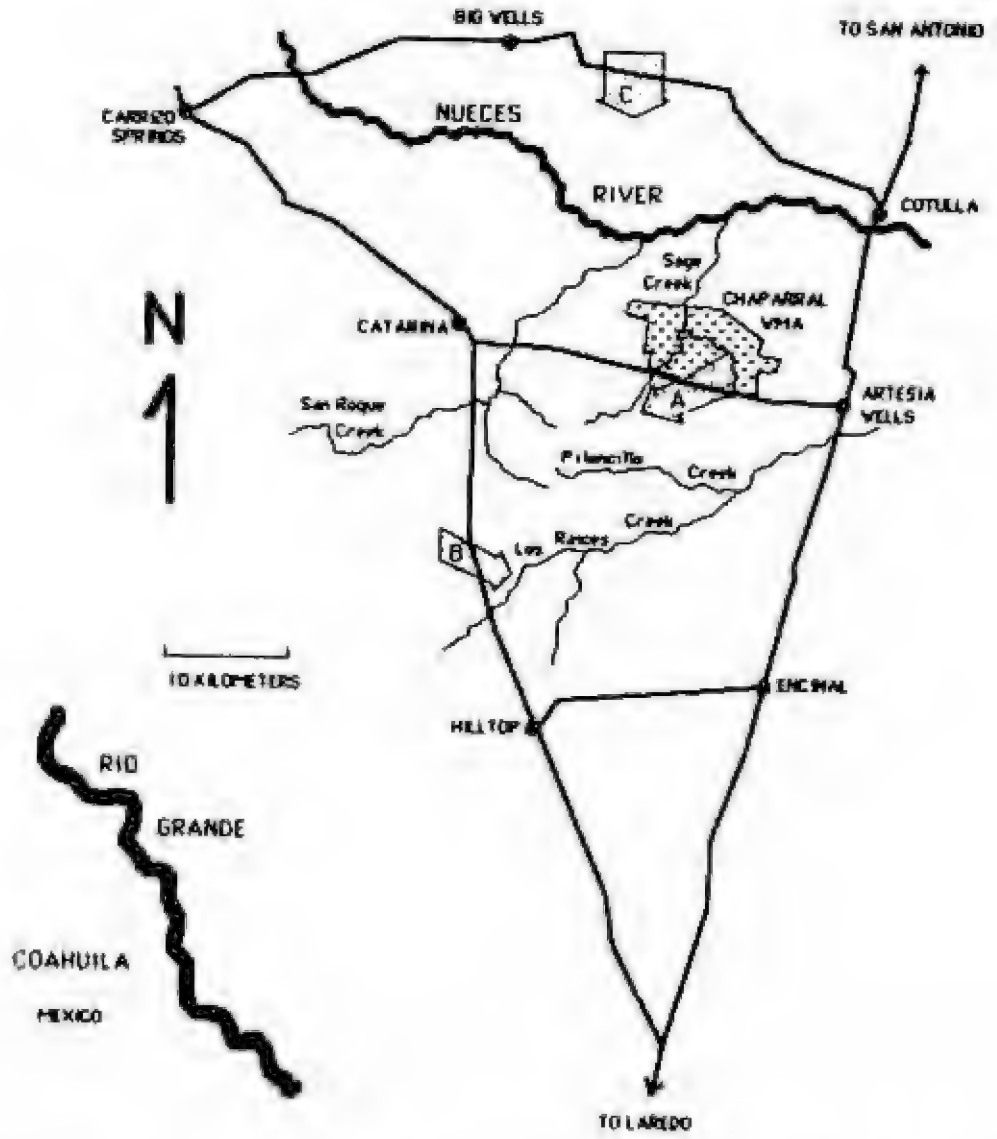

Figure 4

Map of localities discussed in text. Chaparral Wildlife Management Area lies just to the west of Interstate Highway 35 which connects San Antonio and Laredo.

A later survey of the area, carried out on 11 August 1976 by a field assistant, Howard Locker, revealed an additional migration entering the same area south of Catarina (Fig 4, arrow B), a sparse southward migration north of the Nueces River (Fig 4, arrow C), and continued movement at Chaparral (Fig 4, arrow A), but with direction of flight reversing between morning and afternoon.

Both the male-biased sex ratio as well as magnitude of the 1976 Snout Creek outbreak result first from the fact that *C. **pallida***, in contrast to ***Porlieria***, flush new growth in response to defoliation, and second, from the fact that regrowth is not better defended as is the case with some woody plants having inducible defenses (Haukioja and Niemela 1979). Thus the plant can be (and was) defoliated at least twice in one season. It seemed important to pursue further the biology of this plant in order to understand more fully the biology of ***Libytheana*** in this region. I therefore wished to assess the consequences to individual plants of the 1976 defoliation.

In March 1977, the production of new growth was compared between *C. **pallida*** in the 1976 zone of defoliation versus plants not defoliated (Fig 5A), i.e., those away from lower drainage areas. Table 5 shows those results. Twelve bushes had 5 branches of 46 cm length removed for shoot census. Plants living "upland" away from the defoliation zone had more new shoots and approximately 5 times the new

shoot dry biomass as compared to the snout-defoliated sample. Comparison of a single bush known to have been totally defoliated with an untouched counterpart showed a 31-fold difference in new shoot biomass.

By June 1977, many branches alive but defoliated in July 1976 were dead. I walked through Chaparral WMA looking for other such zones and found them. One area along Sage Creek had apparently been defoliated a few years earlier since many *C. pallida* had lost most or all aboveground woody growth. Some were dead, being overgrown by *C. laevigata*, others were producing suckers from the root crown. Had other shrub species been so affected, I would have concluded that fire or herbicide had affected the area.

By 1979, many of the *C. pallida* first observed along the Snout Creek drainage at Chaparral WMA resembled those of Sage Creek (see Fig 6) in having lost most or all aboveground woody growth. Remarkably, the snout butterfly, a small specialist herbivore which would be missing or highly inconspicuous in beat samples from *C. pallida* over at least 90% of the area at Chaparral and during no less than 95% of the years, can periodically reduce the density of the plant, especially in wetter areas. A map of snout-killed or damaged *C. pallida* is a map of the drainage system at Chaparral (e.g., Fig 5B).

There are at least two good reasons for the differential impact of snout butterflies on *C. pallida* in wetter areas. First, these are likely to be the first areas where leafing out begins after rains and the last areas to cease new production. Indeed drainages are often the only areas where new growth can be found on *C. pallida*. Second, other habitat requirements such as nectar plants or diapause sites may be best along these corridors of thick shrubbery (Fig 5B). *Alosysia* (whitebrush) flushes new flowers soon after rains on periodically dormant inflorescences which may last from March to August. This shrub, a favorite nectar plant for snout adults, is very dense along drainage zones and may help concentrate egg laying on *C. pallida* which grow near.

The consequence of snout damage to *C. pallida* in drainage zones is interesting to contemplate. Since these are the prime areas for generating local migrations, it may be that an area would gradually cease to be a source area for migrations as hostplants there are repeatedly defoliated and killed during exceptional episodes of weather. For such an area to return to its previous status as a snout-outbreak zone might require a long period of reinvasion or regeneration by *C. pallida* in bottom areas.

Are upland *C. pallida* defoliated or otherwise seriously affected by snout butterflies? The answer is yes, if the uplands are sufficiently wet and if a large snout population is already present when the *C. pallida* flush new growth. It is such an event that triggers regionwide movements encompassing several thousand square kilometers.

The ingredients for such an event came together in 1977 and 1978. Chaparral WMA was lush but drying out rapidly in June 1977, when I studied the diapausing *Kricogonia* along Sage Creek. From that time until May 1978, Chaparral WMA and the region generally suffered one of the most severe droughts on record. Although

Table 5

Consequences of defoliation by snout butterflies at Chaparral Wildlife Management Area, July 1976, in terms of new growth in mid-March 1977.

	"Creek"	Upland	"Creek"	Upland
	N = 12 bushes 60 branches	N = 12 bushes 60 branches	N = 1 bush 5 branches. Total Defoliation July 1976	N = 1 bush 5 branches No Defoliation July 1976
New Shoots	2282	7192	47	988
New Shoots/ Branch	38	120	9	198
Dry Wt. New Growth/ Branch	0.32g	1.5g	0.08g	2.48g
Biomass Advantage	4.7 ×		31 ×	

Kricogonia was numerous, all other butterflies were extremely rare by early May 1978. I saw a single snout butterfly during six hours at Chaparral on May 7. By late August, an estimated half billion snout butterflies were produced and virtually every ***Celtis palida*** bush was defoliated—***except*** along drainages!

Figure 7 summarizes drought, rainfall, and butterfly migrations at Chaparral WMA during 1978. The steps leading to the massive August flights were as follows. First, an unusual drought presumably eliminated, at least temporarily, parasitoid controls. Next, rains in May and June were well above average, thus allowing rapid increase of the snout butterfly population over 2−3 generations. The result was drainage-zone defoliation and the production of large resident populations of females as well as migratory males during early July. Had conditions returned to normal at this point, 1978 would have been very similar to 1976 in terms of the pattern and extent of snout butterfly outbeak.

However, at the end of July a low pressure system, called tropical storm "Amelia," moved from the Gulf of Mexico into the region, thus insuring that for a third straight month, rainfall would be well above normal. According to Bomar (1983), Amelia was responsible for the 24 hour record rainfall total for Texas, 76 cm in Albany, TX, 4 August 1978. The response by snout butterflies was spectacular. Most *C. **pallida*** at Chaparral WMA and in the region generally were defoliated. Snouts were migrating throughout the region. At Chaparral WMA, they were moving

Figure 5

A. (above) shows *C. pallida* in 1976 defoliation zone being censused for new shoots by T.R.E. Southwood in March 1977. B. (below) shows dense growth of shrubs along drainage zones (usually dry gullies) at Chaparral WMA.

south by tacking into a southwest wind. Sex ratio of migrant population was male biased, but females were clearly a component of the migration when I observed it on 24–25 August 1978. A sample collected near Chaparral contained 85 males and 51 females and a collection from Catarina contained 99 males and 27 females. Eight migrating females were dissected from the Chaparral sample. All eight were mated but none contained mature eggs.

Figure 6

Effects of different levels of defoliation on *C. pallida* by *L. bachmanii* in May 1979. A: J. Longino stands next to a typical "upland" individual which was free of defoliation in 1976 and only partly defoliated in August 1978. B: This bush, along Snout Creek, was defoliated in 1976 and 1978, and when photographed (May 1979), had only a few living large branches (e.g., see cluster of leaves above and behind Longino's hand).

The August 1978 migration culminated about 100 days of astronomical population increase by the snout butterfly. A rough estimate of this increase was obtained as follows. First, it is possible to extract an estimate of the *C. pallida* population from previous Texas Parks and Wildlife surveys on the vegetation of the area. This results in an estimate of 1.56 million hackberry shrubs on the area (an average of 255 per ha, see Table 6). Of these, no less than 85% or 1.32 million were defoliated in August 1978 (this is a conservative guess). From the 1976 defoliation, it was determined that no less than 2000 and 400 snout adults were produced on 3 m diameter and 1.5 m diameter *C. pallida* respectively. Assuming that the 1.5 m bush is approximately average size for Chaparral WMA, the total snout population generated would be approximately one half billion (1.32×10^6 bushes $\times$ 400 snouts·bush^{-1} = 5.28×10^8 snout butterflies). This amounts to about 84,000 butterflies per hectare (8.4 m^2) produced over the emergence period. Can snout butterfly life history characteristics account for this increase?

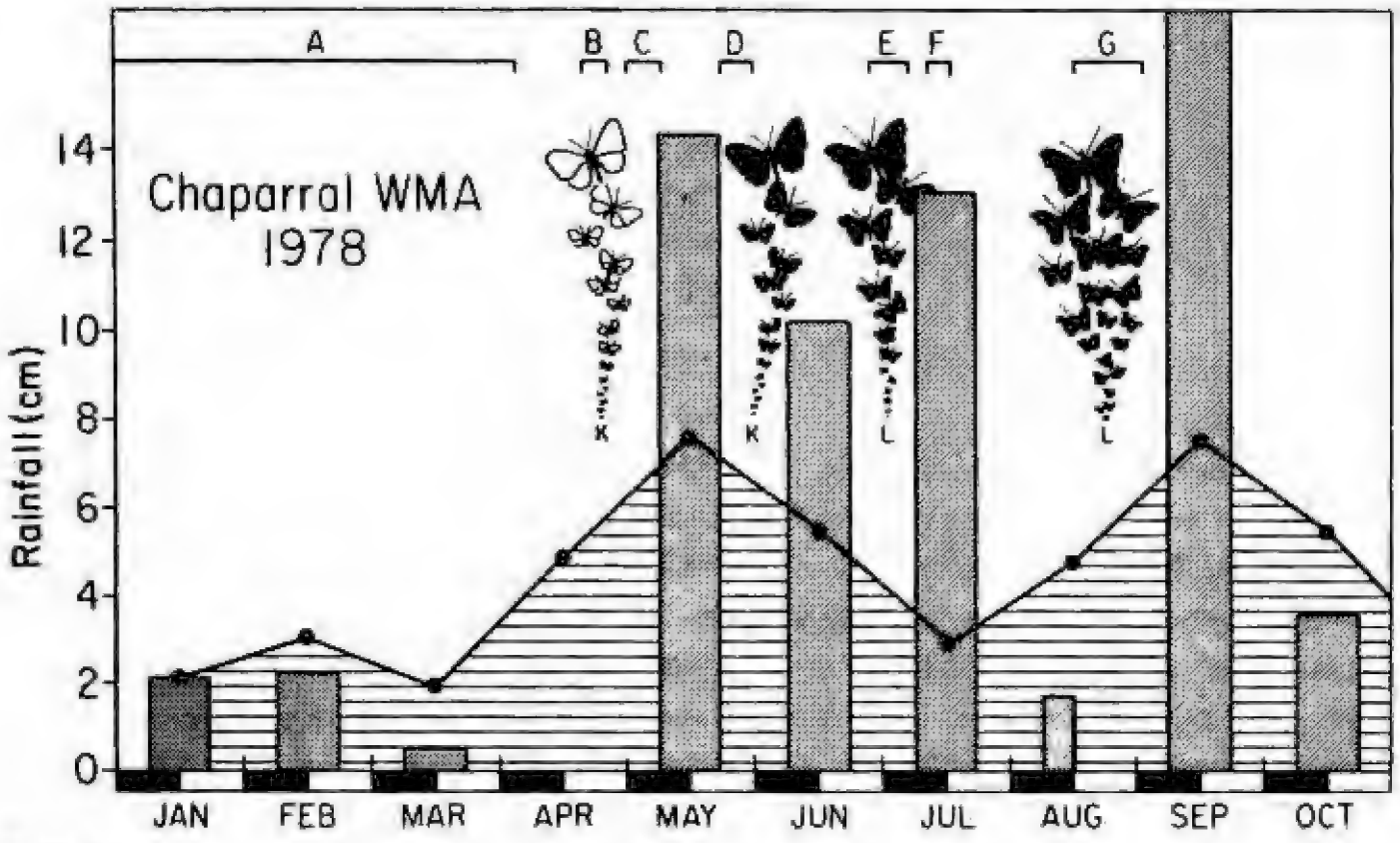

Figure 7

Libytheana **and** ***Kricogonia*** **migrations at Chaparral WMA, 1978, related to longterm averages at nearby Encinal, TX (solid line) and the unusual rainfall of May–July 1978 (stippled bars). Interval A above was a continuation of drought which began in June 1977. Actual migrations are shown as three swarms of black butterflies. During interval C, *Libytheana* were very rare, on the order of one per hectare. During interval D, all-female migration of *Kricogonia* took place. These were the diapausing individuals responding to the May rains (Type II migration). During interval E, *Libytheana* erupted, defoliated *Celtis pallida* along drainages and some migrated locally (Type I migration). During interval F, a large population of *Libytheana* was resident in the area, probably in diapause. This population laid eggs on new growth flushed by late July rains. Less than 20 days later, these had defoliated > 85% of *C. pallida* at Chaparral WMA and entered migratory phase (G). Note that August was relatively dry until the 30th, after migrations were underway. August 30–31 rain totals were added to September's to prevent confusion of causation of the large Type I migration (G). Interval B was not observed in 1978, but was a period of migration by both sexes of *Kricogonia* in 1979, a year with 6.5 cm and 18.3 cm of rain in March and April respectively.**

To answer this question, I assume that snout population growth was virtually unchecked from May to late August 1978, and that it can be described by the simple discrete generation model: $N_t = N_0R^t$. Given a starting population in May 1978 of one female per hectare (N_0) growing to 42,000 females per hectare (N_t) 100 days later in late August 1978, it is possible to see whether biologically realistic combinations of R and t are consistent with such numbers. R, the replacement rate, is simply the average number of female offspring produced per mother in each generation, while t is the number of elapsed generations. Since the egg to adult time for snout butterflies is no less than 16 days, 6 is the maximum value t could assume within the 100 day period and, by observation, t was greater than 2. Thus given t values of 6, 5, 4, or 3, I found that R values of 5.89, 8.41, 14.32, and 34.76 respectively gave the 42,000-fold increase estimated for the Chaparral WMA snout population. These

Table 6

Number of *C. pallida* at Chaparral Wildlife Management Area. Extracted from Ellisor (1970). (Metric conversion of totals are used in text.)

	A	B	C	A × B × C
Zone	Acreage	Woody shrubs/ acre	% *C. pallida*	Total *C. pallida*
Sandy loam	11,570	1,232	9.93	1.33×10^6
Shallow ridge	1,048	1,934	2.70	5.47×10^4
Tight sandy loam	718	3,847	4.53	1.25×10^5
Loamy sand	540	496	3.51	9.4×10^3
Cleared area	1,324	846	3.78	4.23×10^4
Total	15,200			1.56×10^6

values are all well within the reproductive potential of these insects. Thus even larger migratory swarms can be expected under similar conditions from areas having more *C. pallida* biomass.

These crude calculations underscore the efficiency with which parasitoids, predators, predators, poor host quality, host phenology, and other natural controls must be limiting the population growth, and thus the occurrence of conspicuous migratory swarms of *L. bachmanii* over much of its range, most of the time. Host plants of the genus *Celtis* are very common over much of the snout's distribution, yet migrations are extremely rare in the more mesic areas. The impact of the south Texas drought cycle on the natural controls of this species probably accounts for its more frequent migratory behavior there (see Neck 1983). I have assumed this to be true in the present account, but careful studies of larval demography will be necessary to confirm my assumption. The relatively low parasitoid rate of 8% ($n = 658$) in snout pupae collected in the 1976 outbreak zone supports this assumption. Another possibility, not mutually exclusive, is that other species of *Celtis*, which replace *C. pallida* in more mesic areas (e.g., *C. laevigata*) are intrinsically more resistant to herbivory by snout butterfly larvae.

A final aspect of snout migration worthy of further study is the problem of directionality. It is frequently observed that these insects are actively working to move in particular directions, often into light breeze (e.g., Parman 1926, pp. 104–105; Gable and Baker 1922, p. 265) and against substantial wind (e.g., Breland

1948, p. 130; Smyth 1920, p. 259). Southeast and east southeast are very commonly observed flight directions, but most other compass headings are represented (e.g., Table 3). 180° reversals of flight direction between morning and afternoon are occasionally observed (e.g., Breland 1948, Kendall personal communication). However, this may occur in some latter phase of a migration. Thus, at Chaparral WMA 26–28 July 1978, (early) migrations were consistently southwest and west southwest. Two weeks later, 11 August 1978, morning migrations were roughly west, those of afternoon roughly east. Much more data will be required to ascertain the pattern, if any, in migratory direction as it relates to environmental factors such as wind direction and velocity.

SUMMARY

Two shrub-feeding butterflies of south Texas frequently initiate migratory flights. For ***Kricogonia***, the pierid that uses ***Porlieria*** as larval host, migrations may be of two types: Type I migrations follow exhaustion of suitable leaves on larval hostplant early in the season (April). Type II migrations involve the directional movements of previously diapausing populations and are triggered by rainfall. For reasons that are not clear, ***Kricogonia*** migrations are primarily restricted to April–May. Type II migrations are female biased.

Libytheana bachmanii, which uses ***Celtis pallida*** in south Texas, undergoes Type I migration and primarily males are involved. This appears to result from the rapid flushing of new growth by recently defoliated ***Celtis pallida*** which holds females in the area. Type II migrations also occur in ***Libytheana***. Kendall (personal communication) has observed large populations sitting around for weeks prior to large migrations.

Two other categories of migration were identified for snout butterflies: (1) local, involving defoliation, population outbreak, and migration on a scale of a few kilometers and (2) regional, involving widespread defoliation of hosts, population explosions, and migrations over thousands of square kilometers, involving billions of insects. I suspect that both Type I and II migrations can occur at these different spatial scales.

In contrast to ***Kricogonia***, ***Libytheana*** migrates late in the season (July–October). It is not clear why snout butterflies have not been seen moving before June.

Differences between these two butterflies in migratory patterns result from different leafing-out phenologies of hostplants, different degrees of resistance by mature leaves of hosts, and perhaps from differential ability to diapause through south Texas winters or to recolonize from Mexico after harsh Texas winters.

Snout butterflies may be the most significant mortality factor for mature *C. **pallida***, especially in some habitats, and therefore alter the potential of such areas to support subsequent population growth and migration. ***Kricogonia*** appears incapable of completely defoliating ***Porlieria***. ***Kricogonia*** migrations are less conspicuous than those of the snout butterfly because there are fewer ***Porlieria*** than ***Celtis*** and because

a relatively small fraction of *Porlieria* standing crop can be converted into adult *Kricogonia* by their larvae.

In order to develop this relatively complete view of the ecological context of migration in these two insects, I have had to draw from scattered and incomplete information. I have woven facts together with assumptions, extrapolations, and my own intuition for habitats and organisms in south Texas. I prefer to think that this process is akin to the computer enhancement of fuzzy photographic images. Pattern is made clear by replacing grey with black or white. I am not sure what the precise patterns are, but I have tried to generate a coherent picture or model of the system, well summarized by the actual events of 1978 in Figure 7. Hopefully, this model will help organize and focus research that will further elucidate the patterns and their causes.

The danger inherent in such a wonderfully rich biological system which is so poorly known is that there are few facts to constrain imagination. With this in mind, I have avoided any discussions on aspects of *Kricogonia* and *Libytheana* biology that are free of factual information. For example, I did not suggest that the snout (labial palps) on a migrating snout butterfly functions like a divining rod to help it locate some distant oasis. But the fact is, *Libytheana* almost always migrate into a breeze, and since prevailing winds are from the southeast in July and August, migrations are typically seen to be in that direction. *Libytheana* really do seem to be following their snouts for some reason!

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NEW PERSPECTIVES ON THE MIGRATION BIOLOGY OF THE MONARCH BUTTERFLY, *DANAUS PLEXIPPUS* L.

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ABSTRACT

Recent research on large scale movements of monarch butterflies between breeding locations in eastern North America and immense overwintering aggregations in Mexico provides new insights about the biology of this animal in the context of a complex life history which enables a tropical species to exploit a temperate flora. My paper addresses several questions about the monarch's life history strategies. These include: (1) How are the physiological controlling mechanisms of the migration-diapause syndrome adapted to the physical characteristics of overwintering sites in central Mexico, and why is the overwintering range of the eastern population limited to several small and geographically isolated areas of high mountain boreal forests in the transvolcanic range? (2) How do adult lipid dynamics relate to the fall and spring flora, and how important are lipids in fueling winter survival, the distance of the spring remigration, and fecundity during the spring recolonization of North America? (3) Is copulatory nutrient transfer a significant component of fitness in the monarch's spring remigration? (4) Does a two-way migration occur across the Gulf of Mexico via Cuba and the Yucatan to overwintering sites in southwestern Mexico or Guatemala? (5) Are overwintering locations along the Gulf coast important? (6) Is the spring recolonization achieved completely by surviving remigrants, or do their offspring continue to migrate and complete the recolonization? (7) What conservation measures are needed to assure the survival of this unique biological phenomenon?

INTRODUCTION

Contemporary ecological research aims to understand the evolution of life history strategies which involve the optimization of such factors as the timing and numbers of offspring, dispersal and migration (Stearns 1976, Solbreck 1978, Taylor 1980, Denno and Dingle 1981, Dingle 1982). In the ultimate sense, adaptations in life history patterns evolve in relation to density-dependent phenomena such as food resources, competitors, parasites and predators (Southwood 1977, Denno and Dingle 1981, Tallamy and Denno 1981). For most herbivores, food characteristics appear more significant as life history determinants than competition and predation (Chew

1981; Denno and Dingle 1981; Denno, Raup and Tallamy 1981; Lawton and Strong 1981), and these include distribution, quantity, quality, and variability both in space and time (Giesel 1976; Derr 1980; Moeur and Istock 1980; Derr, Alden and Dingle 1981; Moran 1981; Scriber and Slansky 1981; Miller and Dingle 1982; Alstad and Edmunds 1983). Perhaps the clearest examples of adaptations to temporal and spatial variation in food resources are the highly developed migration strategies of many terrestrial avian and insect species which enable them to exploit the periodic abundance of food in temperate zones and later migrate back to overwintering areas in the tropics (Karr 1980, Keast 1980, Baker 1978, Young 1982a).

For example, the monarch butterfly (*Danaus plexippus* L.) utilizes the seasonally abundant *Asclepias* (milkweed) flora of temperate North America as a larval food resource, a flora which underwent an adaptive radiation to 108 known species during the Cenezoic era (Woodson 1954). All *Asclepias* species are perennials, most send up shoots early in the spring, many persist into September and some have increased in numbers as a result of forest clearing and agriculture (Urquhart and Urquhart 1979b, Marks 1983). Milkweeds provide monarchs with an abundant and predictable larval food supply as well as a source of defensive chemicals (cardenolides) which elicit emesis and other noxious effects in vertebrates (reviews in Seiber, Lee and Benson 1983, Brower 1984). The monarch appears to utilize the milkweeds' chemical defense more effectively than other insects (Erickson 1973; Rothschild, von Euw, Reichstein, Smith and Pierre 1975; Blakley and Dingle 1978; Cohen and Brower 1982; Cohen 1983; Brower 1984; Duffey 1970, 1980; Duffey and Scudder 1972; Scudder and Duffey 1972; Isman, Duffey and Scudder 1977a, b) and the ingested cardenolides deter some, but not all, vertebrate predators (J. Brower 1958; Brower 1969; Jeffords, Sternburg and Waldbauer 1979; Fink and Brower 1981; Fink, Brower, Waide and Spitzer 1983; Brower 1984; Brower, Horner, Marty, Moffitt and Villa 1985; Brower and Calvert, in press). Mortality of immature monarchs due to invertebrates varies in space and time (Urquhart 1960, Zalucki and Kitching 1982a), and generally low parasitoid frequencies prevail (Urquhart 1960; Baker 1978, p. 426; Brower, unpublished observations in Massachusetts, California and Florida). It is thought that the high adult dispersal ability of monarchs together with milkweed phenology and geographic distribution allows them to outrun density-dependent buildups (May 1978; Baker 1978, p. 426) in populations of invertebrate enemies (Urquhart 1960, Zalucki 1981b) and congeneric competitors (Brower 1961a,b, 1962b).

The phenology, distribution and abundance of milkweeds as the larval food resource are thus major determinants of the monarch's life history strategy—a strategy which is characterized by a spectacular migration between the summer breeding distribution in the United States and Canada, and overwintering locations along the California coast, the Gulf coast and the volcanic highlands of central Mexico, a proven straight-line southward migration of up to 3,000 km (Urquhart and Urquhart 1978) and a proven return migration of the same individuals of up to 3,500 km (Urquhart and Urquhart 1979a). By being able to undergo reproductive diapause, monarchs escape the northern winter and, by remigrating the following spring, exploit the renewed North American milkweed supply. Indeed, the monarch butterfly

spectacularly bears out the prediction that overwintering in the adult stage is an optimal strategy for a species that must initiate early spring breeding in order to build up its population through several generations (Birch 1948, Dingle 1974b, Hayes 1982).

Several aspects of the modus operandi of the monarch's migratory behavior must be genetically determined, for although the overwintering butterflies themselves return to their general northern breeding range, those that migrate in the fall to precisely located overwintering grounds have never been there; they are at least two and possibly up to five generations removed from their forebearers. Thus the fall migration occurs with no opportunity for information transfer from older experienced individuals such as can occur, for example, in birds.

The majority of butterflies arrive at the overwintering sites as virgins, and most do not mate until winter's end (Table 1). This, together with extensive intermingling during both the fall migration and overwintering period, undoubtedly promotes heterozygosity and breaks down genetic differentiation that has been shown to occur in localized summer breeding populations as a result of the founder effect, genetic drift and/or natural selection (Eanes and Koehn 1978). Indeed, it seems likely that the capacity for monarchs to exploit the diverse array of North American milkweed species is maintained by this behavior, which must effectively prevent any tendencies to race formation involving foodplants. The latter has occurred in some species of nonmigratory lepidoptera including ***Papilio glaucus*** L. which breeds in a range broadly similar to that of the eastern monarchs (Scriber 1983, Diehl and Bush 1984). Monarchs probably oviposit on any ***Asclepias*** species they encounter (Urquhart and Urquhart 1976b). Zalucki and Kitching's (1982b) finding, that various aspects of foodplant quality are more important determinants of oviposition than are the milkweed species per se, supports this contention.

In the past 3 decades, the remarkable biology of the monarch butterfly has stimulated substantial research. As Dingle (1972) pointed out, migration in any animal cannot be understood until viewed in its entirety as a physiological, behavioral and ecological syndrome. My paper develops this theme in the context of a complex life history strategy which enables a tropical species to exploit a temperate flora. Indeed, given the tropical distribution of the 157 recognized species in the Danaidae (Ackery and Vane-Wright 1984), it is not unlikely that the monarch's migratory and highly specialized trophic relationships to the North American milkweed flora have undergone considerable step-wise coevolution (Fox 1981, Futuyma and Slatkin 1983) during the Cenozoic and perhaps even over the last 10,000 years (see also Young 1982b, and below).

Table 1

Mating frequencies in 1283 female monarch butterflies in 21 samples of wild butterflies collected at overwintering sites in California and Mexico, at various locations during the summer breeding season, during the fall migration in Massachusetts, New Jersey, northern Florida, Kansas, and Texas, and from a late fall breeding population in southern Florida. The data are based on the number of spermatophores and/or remnant spermatophore necks dissected out of the bursae copulatrices of females according to the methods of Burns (1928) and Pliske (1973).

Sample Date	Locality	Sample size	Percent mated	Number of Spermatophores in Bursae 0	1	2	3	4	5	6	7	8	9	10
21 Jul–3 Aug 79,	Central MA	41	98	1	8	8	4	8	3	4	1	1	1	2
4–16 Aug 79,	" "	26	77	6	3	3	1	4	4	1	1	1	1	1
25 Aug 79,	" "	18	11	16	1	1	0	0	0	0	0	0	0	0
3–10 Sep 79,	" "	32	6	30	2	0	0	0	0	0	0	0	0	0
16–27 Sep 79,	" "	24	0	24	0	0	0	0	0	0	0	0	0	0
4 Oct 79,	Coastal MA	39	0	39	0	0	0	0	0	0	0	0	0	0
29–30 Sep 79,	Coastal NJ	15	0	15	0	0	0	0	0	0	0	0	0	0
23 Sep 79,	Lawrence KA	61	0	61	0	0	0	0	0	0	0	0	0	0
10 Oct 79,	Austin TX	22	5	21	1	0	0	0	0	0	0	0	0	0
11 Oct 79,	Windemer TX	33	9	30	1	1	0	1	0	0	0	0	0	0
28–29 Oct 79,	Coastal FL	52	29	37	11	2	1	1	0	0	0	0	0	0
14–15 Jan 80,	Alpha 3 MX	99	22	77	17	5	0	0	0	0	0	0	0	0
Southern Florida and California Samples														
5 Dec 75,	Everglds FL	17	88	2	1	3	5	4	1	0	1	0	0	0
17 Dec 79,	Sta Cruz CA	100	37	63	29	6	2	0	0	0	0	0	0	0
15 Feb 80,	Sta Barb CA	100	75	25	44	22	7	0	2	0	0	0	0	0
Additional Mexican Samples														
15 Jan 78,	Alpha 1 MX	50	20	40	9	1	0	0	0	0	0	0	0	0
3 Feb 78,	" " "	101	22	79	18	4	0	0	0	0	0	0	0	0
17 Feb 78,	" " "	100	17	83	17	0	0	0	0	0	0	0	0	0
18 Feb 78,	Alpha 2 MX	102	27	74	25	3	0	0	0	0	0	0	0	0
19-20 Mar 78,	" " "	152	55	68	65	16	3	0	0	0	0	0	0	0
1 Apr 78,	" " "	99	62	38	40	16	3	2	0	0	0	0	0	0

Central Massachusetts = Amherst, Hadley and Northampton, all in the Connecticut River Valley; Coastal Massachusetts = Eastern Point, Gloucester; Coastal New Jersey = Island Beach and Cape May; Coastal Florida = Lighthouse Point, south of Tallahassee; Windemer = Windemere; Everglds = eastern edge of the everglades, northwest of Miami International Airport; Alpha 1,2, and 3 = in our Site Alpha research area as shown in Figures 1 and 2 and described by Brower et al. (1977) and Calvert and Brower (in preparation).

MIGRANT VS. NON-MIGRANT POPULATIONS

Continuously breeding nonmigratory populations of the monarch occur in Mexico east and south of the overwintering sites (Urquhart and Urquhart 1976b), throughout the lowlands of the neotropics, on the Caribbean and Pacific Islands (Urquhart 1960) and in parts of Australia, which the monarch reached in about 1870 (Williams 1930, 1958; Urquhart 1960; Marks 1963; Common and Waterhouse 1972; Smithers 1977; Baker 1978; Wise 1980; Ackery and Vane-Wright 1984).

In contrast to these tropical populations, most North American monarchs undergo reproductive diapause, migrate to overwintering grounds and there spend the winter without breeding. Continuously breeding populations do occur in southern Florida (Scudder 1889; Brower 1961a, 1962b; Urquhart and Urquhart 1976b; Cohen 1983; Table 1, this paper), southern Texas (Urquhart 1960), southwestern Arizona (Funk 1968) and southern California (Downes, in Williams, Cockbill and Downes 1942, Urquhart, Urquhart and Munger 1970) but, contrary to my previous view (Brower 1961a, 1962a), are probably of minor importance to the spring recolonization of the northern habitats. In addition to the well-developed diapause of North American monarchs (Herman 1981), in temperate eastern Australia an apparently less regulated migration–diapause–overwintering syndrome occurs (Common and Waterhouse 1972; James 1979, 1981, 1982, 1983; James and Hales 1983). There is also anecdotal evidence for a fall migration in northwestern Argentina (Hayward 1963, 1969, 1972).

TWO MIGRATORY AND THREE OVERWINTERING POPULATIONS IN NORTH AMERICA

Following Williams (1958), Urquhart (1960) recognized that the monarch butterfly in North America comprises two major breeding populations. The first is a smaller one west of the Rockies which migrates to numerous overwintering locations along the coast of California from north of San Francisco to San Diego and possibly further south (Downes, in Williams et al. 1942; Williams 1958; Urquhart 1960; Urquhart and Urquhart 1977; Tuskes and Brower 1978; Baker 1978; Lane 1984, 1985). The second population is much larger and occurs east of the Rockies to the Atlantic coast. Some of these butterflies overwinter along the Gulf coast, but most migrate to high altitude oyamel fir forests (*Abies religiosa*) of the Sierra Volcanica Transversal, in the states of Michoacán and México (Urquhart 1976a; Urquhart and Urquhart 1976a,b, 1977, 1978, 1979b; Brower 1977; Brower, Calvert, Hedrick and Christian 1977; Brower and Huberth 1977). Data for more than 30 Mexican overwintering colonies indicate a range in size from 0.1 to > 5 hectares (Calvert and Brower, in preparation), and two independent estimates suggest densities of approximately 10 million butterflies per hectare (Brower et al. 1977; Calvert, in preparation).

The numbers of butterflies in the California colonies are two orders of magnitude smaller than in Mexico: a mark, release and recapture study in three colonies determined a range of 40,000 to 95,000 individuals (Tuskes and Brower 1978). Colonies of variable size have also been reported on the Gulf coast (Thaxter 1880, Merriam 1893, Fernald 1939, Williams 1930, Urquhart 1960, Baker 1978), and in a 1981–1982 overwintering colony on Honeymoon Island, north of Tampa, Florida, we estimated there to be a population of approximately 4,000 individuals (Brower and Calvert, in preparation). Whether in fact monarchs overwinter along the Gulf coast other than in Florida is debatable (Mather 1955, Mather and Mather 1958). The timing of first appearances of northward moving monarchs in eastern Florida (Beall 1952) and evidence of winter inhabitants on coastal islands of Georgia (Dennis Owen, personal communication) suggest that some overwintering along the Atlantic coast may also occur.

We have found a few scattered aggregations in Mexico outside the major overwintering area, but these have always been small, have not formed every year, have been subject to high mortality, and in two years an outlying colony (Site Beta in Calvert, Hedrick and Brower 1979) about 40 km north of the Alpha Area (see below) was completely extirpated, possibly by birds (Calvert, unpublished observations). Similarly vulnerable small overwintering colonies of less than 1,000 butterflies have been reported in California 62 km inland from the coast (Fadem and Shapiro 1979) and on the eastern side of the Sierras along streams at canyon mouths in the Saline Valley (Giuliani 1977–1984; Brower, Lane and Shettler, in preparation).

The annual return of monarchs to the same overwintering trees in California is well known (Downes, in Williams et al. 1942; Urquhart 1960). For the past 9 seasons (1976–1985) at our Site Alpha location in the Sierra Chincua, Michoacán, Mexico (Figs 1 and 3), locations of the successive colonies have been separated by less than 3 km, and in three of these years the monarchs formed colonies on virtually identical locations.

THE FALL MIGRATION OF THE EASTERN POPULATION

The Urquharts' (Urquhart 1960, 1966; Urquhart and Urquhart 1978, 1979b, 1980a) tagging program has determined that monarchs of the eastern population fly in a highly directional south to southwesterly path which corresponds to the great circle route towards central Mexico (Schmidt-Koenig 1979; but see this volume). Their direction also corresponds to the prevailing low altitude (< 500 m) winds across much of the eastern and southern U.S.A. in September and October (Anonymous 1968, Bryson and Hare 1974, Kanz 1977, Gibo and Pallett 1979). Funneling through Texas, the fall migrants encounter the ranges of the Sierra Madre Oriental in Mexico. There they appear to change course and follow the mountain ranges in a southeasterly direction, eventually turn southwesterly to cross them and finally reach the central portion of the belt of volcanic mountains which extends across the southern end of the Mexican central plateau between latitudes 19 and 20°N (Calvert and Brower, in preparation).

Figure 1

Aerial view of the *Abies religiosa* boreal forest ecosystem in the Sierra Chincua, Michoacán, Mexico, 17 March 1981. The up-canyon orientation is southeasterly, along Arroyo El Zapatero (Anonymous 1976). The arrow indicates the approximate location of the Site Alpha monarch butterfly overwintering sites at 3,100 m altitude during the 1976–1977 and 1977–1978 seasons. These two sites are also indicated by the two uppermost dots in Figure 3. The highest peak in the photograph is approximately 3,300 m. The photograph was taken from a helicopter provided by Gobernador Cuauhtemoc Cardénas, Governor of Michoacán. (35 mm kodachrome original by L. P. Brower.)

Most butterfly species apparently migrate close to the ground surface in the so-called boundary layer, i.e., that layer in which air movement is less than the butterflies' air speed. This behavior appears adapted to enable them to maintain control of their tracks and not be blown off course (Walker and Riordan 1981; Walker, this volume). According to Urquhart (1960), monarchs can achieve a powered flight velocity of 40 km per hour. As Walker pointed out, this would enable them to maintain a ground layer flight strategy even against fairly strong winds, and Kanz's (1977) data support this contention. Schmidt-Koenig's (1975) and Baker's (1978, p. 428) reanalysis of Urquhart's recapture data indicate mean straight-line fall migration rates of up to 129 km per day, which are well within the limits of boundary layer flight. On the other hand, powered flight is very energy consuming (see below), and Schmidt-Koenig (1979), Gibo and Pallett (1979) and Gibo (1981) have reported monarchs flying with tail winds at ground velocities of 50 km per hour and altitudes

of up to 1250 m above the ground surface. The latter authors have also employed their knowledge of gliding and determined that monarchs conserve energy by well-developed abilities to soar both in topographically determined ascending air currents and in rising thermals.

Gibo's data support the hypothesis that monarchs conserve energy by utilizing tail winds, even though this is an area of controversy in butterfly migration biology (Baker 1978, p. 472; Wehner 1984). Wind systems over the Gulf of Mexico during the fall appear suited to exploitation by the monarchs: surface easterlies blow along the Gulf coast, intersect eastern Mexico at the latitude where our evidence indicates they cross the Sierra Madre Oriental and may well carry them up and over the mountain passes, thereby putting them on target to the overwintering sites (see Figure 2 in Bryson and Hare 1974). The fact that virtually all overwintering monarchs in the Mexican colonies show little evidence of wear (Brower et al. 1977, Brower 1977, Brewer 1982, Kennedy 1984) supports this wind hypothesis.

How monarchs orient and presumably navigate across the complex topography of the United States and Mexico in spite of great potential wind drift (Alerstam 1981) is not well understood (Schmidt-Koenig 1975, 1979; Kanz 1977; Wehner 1984; Walker 1984), nor is their ability to locate the isolated montane overwintering sites. Kanz's and Schmidt-Koenig's data suggest that they do not use time-compensated sun compass orientation. However, sun azimuth orientation per se from 1000−1400 h may be sufficient to keep them migrating in a south-southwesterly direction. Jones and MacFadden (1982) have reported magnetite in adults which may be used in following an internally programmed map (e.g., see Baker 1978, Keeton 1981, Jungreis 1982, Maugh 1982, Schmidt-Koenig, this volume). Interestingly, Ortiz-Monasterio, Sanchez, Liquidano and Venegas (1984) reported a large magnetic anomaly near several overwintering sites and speculated that recognition of such anomalies might signal the terminus points of the fall migration in Mexico. I submit, however, that the most likely explanation for the monarchs' ability to locate the overwintering sites in the states of Michoacán and México is that once they arrive in the correct general area within the latitudinally narrow transvolcanic belt, they are genetically programmed to respond to an appropriate constellation of macroclimatic and microclimatic factors that characterize suitable specific locations.

Monarchs from eastern Canada and the northeastern U.S.A. also fly southwards into Florida and may continue across the Caribbean via Cuba to the Yucatan (Fernald 1939, Urquhart 1960, Urquhart and Urquhart 1976b). However, the Florida peninsula is oriented in a south-southeasterly direction, and the Urquharts' evidence suggests that the majority of migrants on their southwesterly course bypass Florida. Those that do encounter the Gulf coast along the Florida panhandle apparently turn westwards and continue along the land route to Mexico (Urquhart and Urquhart 1976b, c, 1978, 1980a).

Professor Frances James of Florida State University has reported (personal communication) large numbers of fall migrants flying out across the Gulf of Mexico. It is difficult to see how these could survive the nearly 1000 km flight to Yucatan unless they rest on the surface of the ocean, continue flying at night (Scudder 1889;

Williams 1930, 1958; Rankin 1978), or very effectively exploit the October–November cross-Gulf wind systems as many birds do (Buskirk 1980). Alternatively, as suggested by Schmidt-Koenig (this volume), monarchs that appear as if they are flying out over the Gulf may turn back and continue along the westward land route. Urquhart (1960) and Urquhart and Urquhart (1980a) state that monarchs have an apparent antipathy to flying across large bodies of water, and mortality along the Gulf coast in southern Texas during a spring remigration (Heitzman 1962) suggests that it may be a poor strategy. Carefully planned studies are needed to determine the actual fates of the purported cross-Gulf migrants. Systematic observations on the many oil platforms over 100 km offshore could shed light on this question (see Baust, Benton and Aumann 1981), as could lipid analyses of butterflies collected as they arrive at possible Yucatan landing points.

DAYLENGTH AND TEMPERATURE CONSTRAINTS ON MIGRATION, DIAPAUSE, MATING, AND OVERWINTERING

Exploitation of the North American milkweed flora by the monarch is (1) physiologically possible because adults can suspend reproduction during a 4–5 month period and (2) ecologically possible because this reproductive diapause allows them to leave the northern breeding grounds and migrate southward to overwinter in sanctuaries where they can avoid freezing. Barker and Herman (1976), Herman (1973, 1975, 1981, this volume), Rankin (1978), Rankin and Rankin (1979) and other investigators have determined that juvenile hormone (JH) production is controlled by seasonal temperature and daylength progressions which result in a fine tuning of the monarch's migration biology. As fall approaches, cool weather ($< 20°C$) together with shortening daylengths (< 12 hours) result in diminished JH secretion and a reproductive diapause syndrome which includes gonadal repression, reduced sexual behavior, migratory, and gregarious behavior (see also Gossard and Jones 1977, Zalucki 1981a). This diapause appears to break for males in December and females in January (Herman, this volume; Herman, Brower and Calvert, in preparation). In the spring, increasing daylength and temperature stimulate JH secretion which induces maturation of the reproductive glands, courtship, mating and aging. Mating appears to operate as a positive feedback and causes a further rise of JH levels in females (Herman and Barker 1977, see also Chen 1984 for potential analogies with other insect taxa). Gordon and Bandal (1967) and Hayes and Dingle (1983) produced evidence supporting the hypothesis that a similar feedback system may occur in the migratory milkweed bug *Oncopeltus fasciatus* (Dallas). Indeed, the relationship of *Oncopeltus* to North American milkweeds and the proximate and ultimate determinants of its diapause, migration, overwintering and reproduction appear remarkably similar to the monarch (Dingle 1968, 1974a,b, 1978; Rankin and Riddiford 1978; Rankin 1978, this volume).

It appears that once reproductive diapause is broken, gradual warming leads to the spring remigration, whereas sustained hot weather leads to reproductive behavior and a decrease in the migratory tendency. It also appears from the evidence of Urquhart (1960) that high temperature may override short daylength and induce mating and oviposition during the fall migration. However, Lessman and Herman (1981) found that JH is degraded by a specific esterase with a maximum activity corresponding to thoracic temperatures of actively flying monarchs. I thus predict that low initial titers of JH associated with cool weather at the beginning of the fall and spring migrations can be kept low by vigorous flight, i.e., negative feedback may sustain the migratory flight.

To verify some of these postulated relationships, we collected data on mating frequencies from various migrating, overwintering and one winter breeding population (Table 1). Mating dropped off rapidly towards the end of the summer in Massachusetts, and populations of the last summer generation of monarchs captured in Massachusetts, New Jersey and Kansas were in complete reproductive diapause. In two samples from Texas, 5−9% of the females had mated, whereas along the Gulf coast in Florida, 29% had mated, and in a southern Florida sample taken in December, 88% had mated. By 14-15 January, 22% of the females at Site Alpha had mated. Other samples collected at several Mexican sites during January and February 1978 ranged from 17−27% animals mated. By 19-20 March the percent mated in the overwintering colony had risen to 55% and further increased to 62% in early April. The hypothesis of temperature-induced mating behavior agrees with the thermal regime at Alpha: daily maximum temperatures of 20°C were only exceeded in mid-March which coincided with the beginning of increased mating activity, as well as the commencement of the remigration (Calvert and Brower, in preparation).

The precise modus operandi of daylength, temperature, and their interactions in cuing and regulating diapause, migration and overwintering behavior of the monarch is not well understood (e.g., see Tauber and Tauber 1976). Rates of change of daylength, the positive or negative aspect of the change and the equinoxes which coincide with the populational midpoints of both the southward and northward migration are probably all important, at least in the eastern population (Malcolm et al., in preparation). It is likely that the relationships of these planetary cues to the migration syndrome in the western population are substantially obscured by the higher temperatures in California.

TEMPERATURE CONSTRAINTS ON MIGRATORY ROUTES AND OVERWINTERING LOCATIONS

The postulated overriding of reproductive diapause by high temperatures is consistent with the findings that populations on the tropical margins in the temperate zone often continue breeding throughout part or all of the winter, as reported in Arizona, California, Florida and Texas (Fernald 1939; Urquhart 1960; Brower 1961a, 1962b; Funk 1968; Urquhart et al. 1970). An early December sample of butterflies collected in a several acre field of semi-senescent *Asclepias curassavica* plants on the

eastern edge of the Everglades also indicated an actively breeding population: 88% of 17 females were mated (Table 1), 5 mating pairs were seen, and 13 of 15 females contained mature eggs (Brower, unpublished data).

I suggest that the potential for the breaking of diapause by high temperature has been of paramount importance in determining the fall migratory routes and in delimiting the climatic characteristics of the overwintering localities. Thus if the butterflies failed to turn westward across the Sierra Madre Oriental (which they appear to do at approximately latitude 23°N, Calvert and Brower, in preparation), they would encounter the tropical rainforest along the coastal plain which begins at approximately latitude 21°N (see Arbingast et al. 1975). Similarly, if they overflew the transvolcanic range for as few as 30 km, they would end up in the tropical Balsas Basin. Because of the high temperatures of these areas, the individual fall migrants would become reproductively active, their offspring would overwhelm the local milkweed populations, and the numbers of surviving adults would be far fewer than the numbers of migrants that arrived in the fall. A small proportion of migrants to the transvolcanic area probably do become reproductively trapped in this way (Vázquez, Perez and Perez, personal communication) and thereby lose their ability to recolonize North America via the spring remigration.

Monarchs that fly southwards through Florida into the Caribbean Islands or into the Yucatan must have this same fate. The Urquharts' (1976b) proposed migratory route via Cuba and the Yucatan Peninsula to ***and*** from the mountains of Mexico and Guatemala south of the Isthmus of Tehuantepec thus seems unlikely.

GEOGRAPHICAL, CLIMATIC AND VEGETATIONAL CHARACTERISTICS OF THE MEXICAN OVERWINTERING AREAS

The Transvolcanic Range of Mexico extends for about 640 km across Mexico between the 19th and 20th parallels and constitutes a unique biotic province in North America (Moore 1945, Goldman and Moore 1946). It appears to have had its origin in two periods of volcanism, first during the Miocene, which affected all of Mexico, and then during the Pliocene through the present which has accounted for most of the uplift as well as the volcanic peaks of the region (Thayer 1916, Garfias and Chapin 1949). Thus the Mexican overwintering phenomenon may be of very recent origin (see Duellman 1965 for a discussion of the geological, vegetational and climatic characteristics of Mexico during the Pleistocene). The higher massifs in this range support a disjunct series of very limited boreal forest ecosystems dominated by ***Abies religiosa*** (Leopold 1950; Figure 3 in Duellman 1965; Sanchez 1976; de Miranda, Garcia and Gyves 1977; Anonymous 1981a,b). All major overwintering colonies that we have found occur in these fir forests at isolated sites restricted within a remarkably small area of approximately 3330 km^2 between 19°10′ and 20°00′ north latitude and 100° and 100°20′ west longitude. The sizes of approximately 30 colonies ranged from about 0.1 to more than 5 ha (Calvert and Brower, in preparation). Whether the butterflies also overwinter (or did so prior to forest degradation) in various fir refugia

to the east and west of this area is unknown, but is suggested by the data of Urquhart and Urquhart (1980a). The discovery of further overwintering sites in the Transvolcanic Range might profitably follow the Bosque de Oyamel key in the recent detailed 1:1,000,000 vegetation maps of Mexico (Anonymous 1981a,b; see also p. 115 in de Miranda et al. 1977).

This rich fir forest ecosystem (Fig 1) occurs on the volcanic mountain massifs in a belt between approximately 2400−4000 m altitude (Duellman 1965) which is frequently enshrouded in fog, especially during the summer wet season. Below the firs, various species of pines and oaks dominate, whereas above the firs the same pines again occur, but without the oaks (Leavenworth 1946, Eggler 1948, Goldman 1951). All the colonies that we have found occur only in those fir forests which extend to the mountain tops. Their apparent absence from the fir belts on the higher mountains (Calvert and Brower, in preparation) may be due to cold air drainage. However, Urquhart and Urquhart (1980a) have alluded to a colony on one higher massif, possibly Nevado de Toluca (maximum altitude 4560 m, Duellman 1965).

Although freezing and snow occur at and above the altitude of the fir belt during the winter (Goldman and Moore 1946; Duellman 1965; Mosino-Aleman and Garcia 1974; Urquhart and Urquhart 1976b, 1980a; Calvert, Zuchowski and Brower 1983, 1984), the temperature extremes characteristic of the northern boreal climate are moderated because of the tropical latitude. As a result, the area has substantial thermal stability (Mosino-Aleman and Garcia 1974) which makes it possible for the monarchs to survive the overwintering period at relatively low temperatures in a state of reproductive torpor and reduced, but not total, inactivity (Calvert and Brower, in preparation).

Yearly observations beginning in the fall of 1977 through March 1984 indicate that the butterflies arrive at the overwintering areas during November to early December and by January consolidate into one or more densely packed colonies. By late February the colonies begin to break up and by mid-March (not at the end of January as per Urquhart and Urquhart 1976a, see also Urquhart and Urquhart 1980a) the butterflies commence their remigration northward, with all departing by early April. The departure is spectacular.

The overwintering period lasts for approximately 135 days (15 November−1 April, Brower and Calvert, in press) and coincides with the dry season which is characterized by increasing aridity and variance in the daily temperature regime (Mosino-Aleman and Garcia 1974, Arbingast et al. 1975). Survival of the monarchs depends on a balance of climatic factors which requires that the weather be (1) cold enough to maintain the butterflies in a state of reproductive torpor, but not so cold as to kill them, (2) warm enough to allow them to maintain the integrity of their clusters, but not so warm as to result in excessive activity and (3) wet enough to prevent desiccation and forest fires, but not so wet and cold as to cause excessive inactivity.

Because of the high altitude, clear nights result in heavy frosting of surfaces which are exposed to the sky, and butterflies which are not shielded by the intact forest canopy may be killed by inoculative freezing (Brower et al. 1977; Calvert and Brower 1981; Calvert, Zuchowski and Brower 1982, 1983, 1984; Calvert and Cohen

1983). The increasing dryness is frequently moderated by adiabatic cloud formation, showers and fog drip which also reduce nocturnal heat loss. Major storms also occasionally bring considerable precipitation into the area. In three of our seven seasons of periodic observation (1976–1983), these were accompanied by gale force winds, heavy rains, hail and/or snow which soaked and dislodged many butterflies from the branch clusters. In January 1981 a series of storms over a ten-day period resulted in a cumulative snowfall of 43 cm, caused temperatures to drop as low as −5°C and killed an estimated 2.5 million monarchs (Calvert, Zuchowski and Brower 1983, 1984).

These field observations confirmed laboratory estimates of lethal low temperatures for monarchs (Urquhart 1960) and make extremely unlikely the 19th century hypothesis (Riley 1877; Scudder 1889; Klots 1951; Baker 1978, p. 427–428; Baker 1981, p. 74) that up to 30% of the population survives northern winters by hibernating as adults or chrysalids beneath bark or in tree crevices. Baker's (1978) adherence to this hypothesis was based on reanalysis of spring migration rates in California, from which he concluded that remigrants from Mexico cannot fly far enough to reach the northern parts of the range by early summer. We shall see below that the monarchs' spring migration physiology in the eastern range is sufficiently different from that in California to negate this argument, as are the great spring flight distances determined by recaptures in New York, Iowa and 5 other U.S.A. localities of monarchs previously tagged in Mexico (Urquhart and Urquhart 1979a).

While cool temperatures and moisture are essential during overwintering, sunny days are also important. At temperatures near freezing, butterflies in the shade, even if in clusters, are unable to raise their body temperatures above ambient levels (May 1979; Casey 1981; Chaplin and Wells 1982; Willmer 1982; Masters, Brower and Malcolm, in preparation). However, by basking in direct sunlight, the butterflies can passively warm their thoracic muscles to flight temperature, 15.5°C (Kammer 1970, Kammer and Bracchi 1973, Wasserthal 1975), and regain their positions in the clusters when knocked down by storms, by birds or mammals foraging in the trees, by falling branches or by their dramatic response to smoke (Brower et al. 1977). If the temperature is less than about 13°C, and the butterflies are grounded on an overcast day or in a shaded area, they flap about on the ground and then settle into a shivering phase which warms them sufficiently to crawl up onto any available vertical surface (Brower et al. 1977, Calvert and Cohen 1983).

Basking must also be advantageous because it allows the butterflies to conserve energy when they fly out and back to the colony during periods of sustained dry weather to redress their water balance. During clear cold days in January 1980, we observed tens of thousands of monarchs drinking in sunlit patches of the mosaic lighting along Arroyo La Plancha stream in the Site Alpha area. The importance of basking while they drink from the cold stream was indicated by the butterflies' complete avoidance of shaded areas and by the fact that they rapidly flew to another sunny position if experimentally shaded. Basking not only obviates the warm-up shivering, but it also maintains instant flight readiness in the event of a predator attack.

Our observations after storms when the ambient temperature remained below 5°C indicate that crawling is of great importance to the butterflies. To date, thermoregulatory studies of shivering in butterflies have focused on its role in raising thoracic temperature to the flight threshold (Kammer 1970, 1971). The physiology of raising body temperatures to a crawling threshold has been neglected, as have the energetic costs thereof.

The significance of the 15.5°C temperature was evident from thermograph recordings at Site Alpha during the 1978–1979 overwintering season (Brower and Calvert, in press): 15.5°C was not exceeded in the shade until 10 March when the colony began breaking up and the butterflies commenced their northward remigration. Once this ambient temperature is exceeded, the butterflies can maintain instant flight readiness, irrespective of the degree of cloud cover.

In summary, the high altitude fir forests in this narrow zone between 19° and 20°N latitude of Mexico's Transvolcanic Belt provide a cool climate, stable minimum nightly temperatures and a balance of sufficient moisture and sunshine which seem ideally suited for the survival of these densely packed monarch overwintering colonies.

ADULT LIPID RESERVES

Data for total lipid content of fall migrants in the eastern population indicate considerable variability. Mean values per butterfly from Ontario were 141 mg (Beall 1948), from Missouri 131 mg (Brown and Chippendale 1974) and from West Virginia 100 mg (Cenedella 1971). During the 1979–1980 season, Walford (unpublished) and Walford and Brower (in preparation) found that the mean lipid contents of fall migrants in Massachusetts, New Jersey, Kansas and Florida increased by 500% as the butterflies approached the overwintering sites in Mexico (Fig 2C and D). This is possible because of the abundance of fall blooming composites along the Gulf coast, in Texas, northeastern Mexico (Rickett 1969) and in the general vicinity of the overwintering areas (Calvert and Brower, in preparation). The geographic and temporal variability of these data indicate that nectar feeding and conversion of the carbohydrates to lipids is a dynamic process which must be affected by annual variation in nectar availability and perhaps also by weather patterns prevailing during the migration period. Consequently, the hypothesis that monarchs base their fall migration largely on fuel reserves built up by feeding on nectar ***before*** flying southward from their breeding grounds (Urquhart 1960) is no longer tenable, at least for the eastern population.

Brown and Chippendale (1974), Tuskes and Brower (1978) and Chaplin and Wells (1982) reasoned that residual lipids at the end of the overwintering season must be crucial as fuel for long distance flight and for reproductive success of the spring remigration. Because nectar supplies progressively deteriorate from December through February (Calvert and Brower, in preparation) and the butterflies so vastly outnumber the flowers (Brower et al. 1977), the monarchs cannot renew their lipid reserves. Walford and Brower (in preparation) found that mean lipid contents dropped from 89

mg in January to 59 mg in March (Fig 2E and F). Thus lipids appear critical to maintain the overwintering activities, and any factors increasing the activities of the butterflies in their overwintering sites must reduce their ultimate fitness by causing lipid depletion.

Gibo and Pallett (1979) estimated that during their leisurely, flapping, southward migratory flight for which Urquhart (1960) estimated a rate of 18 km per hour, monarchs would consume about 3.25 mg of lipid per hour, i.e., would have a range of about 5.54 km per mg of lipid. If all of the remaining lipid at the end of the overwintering season (mean = 59 mg, maximum = 150 mg, Walford and Brower, in preparation) were to be used in this leisurely flight mode without soaring or using tailwinds, the average to maximum range of the spring remigration would be 326–831 km. Because lipids are mobilized into yolk production (Pan and Wyatt 1976), potential range and fecundity must conflict. Following Urquhart (1960, 1966), Johnson (1969), Rankin (1978), Rankin and Rankin (1979) and Turunen and Chippendale (1981) have assumed that little nectar foraging takes place during the spring migration. There are in fact no data supporting this hypothesis, which was deduced from observations made before the discovery of the Mexican overwintering sites (= 9 January 1975, Urquhart and Urquhart 1977, p. 1584) and it seems extremely unlikely in view of the energy demands upon the spring migrants. Indeed, energy requirements may be even greater if Urquhart (1960) is correct in his contention that the spring migration is by maximally powered, rather than by soaring flight. The Urquharts' (1979a) spring recoveries of several monarchs up to 3,500 km from where they were marked in Mexico could not possibly have been individuals which used only powered flight and old lipid reserves. In fact, there is a resurgence of blooming composites in the overwintering area during the time the monarchs leave in March and April, and the butterflies do feed upon these flowers extensively (Calvert and Brower, observations). Finally, Heitzman's (1962) data (apparently the first report of the spring remigration in Mexico) suggest extensive nectaring and leisurely flight along the Sierra Madre Oriental migration route back into Texas.

The relationships of floral phenology, nectar resources, migration dynamics (including modes of flight and the possible exploitation of wind patterns), fecundity, and recolonization potential during the spring migration are in need of quantitative study (cf. Dingle 1972, Gilbert and Singer 1975, DesGranges and Grant 1980, Slansky 1980, Grant 1983).

POTENTIAL REFUELING OF FEMALES THROUGH COPULATORY NUTRIENT TRANSFER

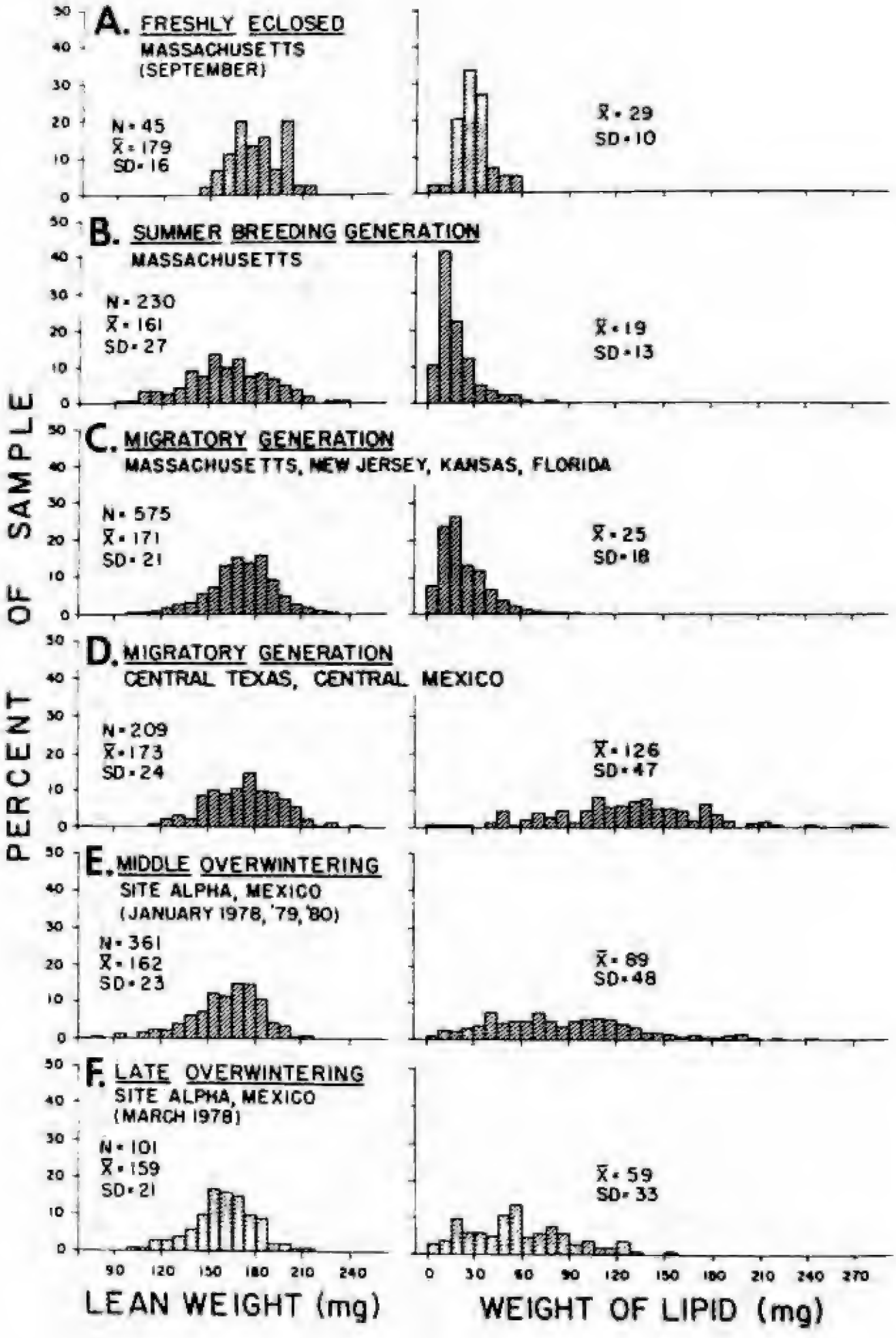
In various insect species, repeated copulation can increase the fecundity of females by transferring considerable male biomass including amino acids, amino acid derivatives, proteins, carbohydrates and lipids (Davey 1965, Leopold 1976, Friedel and Gillott 1977, Thornhill 1979, Boggs and Gilbert 1979, Lederhouse 1981, Chen 1984). Monarch butterflies mate repeatedly (Downes, in Williams et al. 1942; Pliske 1973, 1974; Brower et al. 1977, Table 1), and in the California overwintering colonies frenzied mating activity reaches a crescendo immediately preceding the spring dispersal with the result that over 95% of the females have been found mated from

one to 7 times before they leave the colonies (Downes, in Williams et al. 1942; Hill, Wenner and Wells 1976; Tuskes and Brower 1978; Chaplin and Wells 1982). Herman (1981) hypothesized that this increases the success of the female remigrants and represents a true male parental investment, contrary to the conclusion of Thornhill and Alcock (1983, p. 66). Achey (unpublished) demonstrated that male monarchs also transfer cardenolides in the spermatophores, which may provide an additional increase in female and offspring fitness (see Brower 1984; see also Meyer, Schlatter, Schlatter-Lanz, Schmid and Bovey 1968 for cantharidin transfer in the spanish fly).

Multiple mating by monarchs in California appears to be a response to the rapidly warming spring which mediates JH production both directly and indirectly via positive feedback through the stimulatory effect of the reproductive behavior (Herman and Barker 1977). Moreover, the rapid progression of reproductive maturation in the males appears to result in their senescence so that many disperse and die without accompanying the females on the remigration. However, Shapiro, Palm and Wcislo (1981) did capture both sexes in a small sample in the Sierras early in the season so that at least some males do apparently accompany the females.

In Mexico, the mating frequency also increases as spring advances, but with less intensity so that in April over 30% of the females leave without spermatophores in their bursae (Table 1). Moreover, both sexes leave the Mexican colonies (Brower and Calvert observations), and the few data that exist on returning migrants captured in the United States support the hypothesis that they continue migrating northward together (Urquhart 1960, pp. 318–319, 1976b, Urquhart and Urquhart 1979b). Urquhart (1976b) speculated that the males do not fly as far north as the females. A collection of migrants made by F. James along the Gulf coast south of Tallahassee, Florida from 29 March–3 April 1979 included 9 males and 7 females. Another collection in north central Florida on 7 April 1984 (at the Cross Creek locality cited in Malcolm et al. in preparation) included 3 males and 3 females in moderately worn condition. The origin of these butterflies is, however, unknown; they could have come from Mexico or from overwintering roosts along the Gulf coast. It is unfortunate that the Urquhart's (1979a) did not indicate sexes or dates of the 7 spring remigrants marked at the Mexican overwintering sites and recaptured in northern Mexico, Texas, Mississippi, Florida and New York.

Females which fly northwards from Mexico into the United States encounter a slow warming trend with the result that JH titers must rise more gradually than in California. Consequently, adult aging and egg maturation must proceed more slowly, occasional nutrient transfer from males to females along the migratory routes could occur, and the butterflies might therefore be able to migrate much greater distances. It would be useful to develop optimality models which relate geographical temperature and wind regimes, time, energy expenditures and gains, migratory distance, degree of dispersion, nutrient transfer and lifetime fecundity of the monarch (e.g., see Pyke 1981).


A. FRESHLY ECLOSED
MASSACHUSETTS
(SEPTEMBER)
N = 45
X̄ = 179
SD = 16
X̄ = 29
SD = 10
B. SUMMER BREEDING GENERATION
MASSACHUSETTS
N = 230
X̄ = 161
SD = 27
X̄ = 19
SD = 13
C. MIGRATORY GENERATION
MASSACHUSETTS, NEW JERSEY, KANSAS, FLORIDA
N = 575
X̄ = 171
SD = 21
X̄ = 25
SD = 18
D. MIGRATORY GENERATION
CENTRAL TEXAS, CENTRAL MEXICO
N = 209
X̄ = 173
SD = 24
X̄ = 126
SD = 47
E. MIDDLE OVERWINTERING
SITE ALPHA, MEXICO
(JANUARY 1978, '79, '80)
N = 361
X̄ = 162
SD = 23
X̄ = 69
SD = 48
F. LATE OVERWINTERING
SITE ALPHA, MEXICO
(MARCH 1978)
N = 101
X̄ = 159
SD = 21
X̄ = 59
SD = 33
PERCENT OF SAMPLE
0 10 20 30 40 50
90 120 150 180 210 240
0 30 60 90 120 150 180 210 240 270
LEAN WEIGHT (mg)
WEIGHT OF LIPID (mg)

SPRING RECOLONIZATION OF NORTH AMERICAN MILKWEED

Other than the ability of monarchs to find patches of milkweed no matter how isolated and recondite (Shapiro et al. 1981, Shapiro 1981), we know little about the routes, timing, or the behavior of the butterflies during their spring remigration in either the western or eastern North American populations.

In the eastern population, four processes have been hypothesized to explain how the spring remigration results in recolonizing the breeding grounds—(1) ***single recolonization***: spring remigrants recolonize the entire eastern range from the Gulf coast northwards to Canada and then die (Fernald 1939; Williams 1958; Urquhart 1960, 1966); (2) ***successive brood recolonization***—spring remigrants recolonize the southern states eastwards to Florida and die, leaving subsequent generations to disperse and recolonize the northern range (Riley 1880, Klots 1951, Howe 1975, Kanz 1977, Urquhart 1976b, Baker 1978, Pyle 1981, Herman 1984 and this volume); (3) ***combination recolonization***: spring remigrants reach variable distances north and eastwards and recolonization is accomplished partly by this direct remigration and partly by successive brood recolonization (Urquhart 1960, p. 321, 1966; Brower and Huberth 1977); (4) ***dual recolonization***—Mexican remigrants recolonize the central and western part of the range, while remigrants from the Gulf coast colonies recolonize areas south and east of the Appalachian mountains (Malcolm et al., in preparation); this could occur by processes 1 and/or 2.

Possible alternative individual migration strategies are that spring remigrants: (1) oviposit upon any milkweeds they encounter along a continuous northeasterly flight path, including the extensive milkweed flora of northeastern Mexico (Woodson 1954) or (2) delay oviposition until they arrive in the vicinities of their original breeding grounds. As indicated above, reproductive studies provide support for the first hypothesis: oogenesis occurs slowly at low temperatures so that it is likely that females leaving Mexico will initially be unencumbered by large numbers of eggs, but will have an increasing rate of egg maturation as seasonal temperature, daylength, and available larval food increase as they progress northwards. The hypothesis that monarchs "home" to their prior summer's original breeding sites seems untenable, but it cannot be rejected on the basis of existing evidence (Eanes and Koehn 1978).

Figure 2

Histogram of the lean weights and total lipid contents of 1501 monarch butterflies collected at various times and locations during the summer and fall of 1979 and from overwintering sites in Mexico during the winters of 1978–1980. The data include males and females collected on the dates and areas in Table 1, freshly eclosed butterflies from chrysalids collected during September in western Massachusetts in 1977 and 1979 (A) and a sample collected on 31 October 1977 in San Javier del Oro along the migration route in north central Mexico (included in D). The butterflies were dried, weighed and ground, after which the lipid was extracted from individual butterflies in petroleum ether and weighed; lean weights = dry weight − weight of the lipid (from Walford and Brower, in preparation).

Monarch adults and/or their eggs first appear in Texas in mid-March to early April (Urquhart 1976b), in the Gulf states by late March–early April, in Georgia in March and April (Harris 1972), in Virginia by mid–late April (Clark and Clark 1951) and in New England and southern Canada by May–early June (see also Scudder 1889, Williams 1930, 1958, and Urquhart 1960). Our data from north central Florida (approximately 29°30'N) indicated peak oviposition on *A. humistrata* Walt. in early April in the springs of 1982 through 1984 (Cohen and Brower 1982; Malcolm et al., in preparation; Brower, unpublished data, 1984). Oviposition records made on *A. viridis* Walt. during the spring of 1982 and 1983 in central Louisiana by Dr. Steven P. Lynch of Louisiana State University at Shreveport (personal communication) agree with this timing. In the midwest, first arrivals were reported in Polk Co., Wisconsin (45°N–46°N) in late May just as *A. syriaca* was sprouting (Barker and Herman 1976), in Minnesota in late May–early June (Herman 1984) and peak oviposition occurred on this milkweed on 9 June in Wisconsin at latitude 43°N (Borkin 1982). By midsummer, monarchs are widely dispersed throughout much of the United States and southern Canada (Beall 1948, Williams 1958, Urquhart 1960, Brower 1977, Rankin 1978, Borkin 1982). It is possible that the butterflies produced in the first spring generation in the south may exploit the early summer surface tropical airstream and thereby disperse both northward through the Great Plains and northeastwards in the U.S.A. and Canada (see Figure 4 in Bryson and Hare 1974, Kanz 1977).

Spring monarchs that fly northeastwards through Texas and on up the Mississippi Valley to Missouri and Kansas (40°N) must frequently encounter the abundant *A. viridis*, while those migrating farther east along the coastal plain from Florida and northeastward along the Atlantic coastal plain from Georgia to Cape Hatteras westwards to the Appalachians must most frequently encounter *A. humistrata* (Woodson 1954; Brower 1961a; Nishio 1980; Nishio, Blum, Silverton and Highet 1982). Farther north (beyond latitude 35°N), and from eastern Kansas to the Atlantic Ocean, migrants must most often encounter *Asclepias syriaca*, the most abundant eastern milkweed (Woodson 1954). The observations compiled by Urquhart (1960) indicate that it is the major larval food resource from early summer through the end of the breeding season (see also Urquhart and Urquhart 1979b, 1980a; Borkin 1982). Most fall migrants, and therefore overwintering monarchs, probably will have fed as larvae on this milkweed. Farther west, *A. speciosa* is an ecological equivalent of *A. syriaca* and is also an important foodplant of the monarch (Brower, Seiber, Nelson, Lynch and Holland 1984).

RECOLONIZATION POTENTIAL OF GULF COAST MONARCHS

Published comments on the relative contribution of spring remigrants from Mexico and the Gulf coast to monarch recolonization of eastern North America are entirely speculative and hypothetical (Urquhart 1960, 1966; Baker 1978; Eanes and Koehn 1978; Urquhart and Urquhart 1976, 1979b). However, monarchs that overwinter along the Gulf coast may be important. Beall and Williams (1945) and Beall (1946) reported that individuals collected during the winter in Florida and Louisiana had shorter wing lengths and lower fat reserves than did summer generation and autumn migrants in Ontario. These authors did not have access to monarchs in the recently discovered overwintering sites in Mexico. We have determined that these

animals contain large amounts of fat (Fig 2) and also long wings (Walford and Brower, in preparation). Beall's smaller and fat-deficient butterflies may have represented either less fit individuals stranded during the fall migration (Tuskes and Brower 1978) or a special wintering Gulf coast population selected for reduced wing loading (Gibo and Pallett 1979). Such a population might have a temporal advantage in being able to exploit the early spring milkweeds before the remigrants from Mexico arrive. It is not without interest that individuals with reduced wing loads also occur in Florida populations of the milkweed bug (Dingle, Blakely and Miller 1980). Indeed, Gulf coast overwintering monarch colonies may represent part of a mixed life history strategy (Istock 1978) with weak maintenance of reproductive diapause by temperature and photoperiod.

One way of resolving the importance of the Gulf coast population is to utilize a recently developed method of cardenolide fingerprinting, a powerful new application of thin layer chromatography which enables the identification of the *Asclepias* hostplant species that individual adult monarchs previously fed upon as larvae. Monarchs reared in California on ***Asclepias eriocarpa*** Benth. (Brower, Seiber, Nelson, Lynch and Tuskes 1982), ***A. speciosa*** (Brower et al. 1984) and ***A. californica*** Greene (Brower, Seiber, Nelson, Lynch, Hoggard and Cohen 1984), and monarchs reared on ***A. humistrata*** and ***A. viridis*** in Florida have characteristic cardenolide fingerprints (in preparation). Preliminary determination of the fingerprint of monarchs reared from ***A. syriaca*** (Brower 1984) is similar to monarchs reared on ***A. speciosa*** in California (Brower et al. 1984). Since most fall migrants in the eastern population will have fed upon these two species, we can use cardenolide fingerprinting to determine whether spring breeders in the southeast have returned directly from Mexico or the Gulf coast sites, or whether they represent monarchs of the first spring generation which fed upon ***A. humistrata*** or ***A. viridis***, both of which contain very large amounts of cardenolide (Nishio, Blum and Takahashi 1983; Brower and Malcolm, in preparation). It is possible that monarchs exploit these two very toxic spring milkweeds in the south as soon as possible during their remigration with the result that the first spring generation is well defended against naive fledgling birds (Welty 1982, Brower 1984).

OPTIMAL BREEDING TEMPERATURES IN RELATION TO MILKWEED DISTRIBUTION

Temperature limitations upon developmental rates of monarchs appear critical to the spring and summertime breeding at various latitudes in the U.S.A. and Canada. Barker and Herman (1976) found that maximal ovarian development occurs at 28°C, and Rawlins and Lederhouse (1981) determined that the developmental zero temperature for monarch larvae was about 12°C, whereas the larvae die at constant ambient temperatures above 35°C. Most rapid larval development occurs between 25–30°C which is similar to the adult oogenesis optimum (see also Zalucki 1982, Zalucki and Kitching 1982b).

Urquhart's (1966) map showing the major concentration of summer breeding in the eastern population excludes the southern states, and data from north Florida (Malcolm et al., in preparation), together with those of Brower (1961a, 1962b) substantiate reduced summer breeding in the south, even though several milkweed species are available and continue to be extensively fed upon by ***Danaus gilippus berenice***. The optimal summer breeding temperatures for monarch development in eastern North America appear to coincide with the temperatures prevailing in the areas which include the most abundant ***Asclepias*** growth. In the southern U.S.A., milkweeds occur as less well-defined and patchy resources (Dingle, Alden, Blakely, Kopec and Miller 1980; Dingle, Blakely and Miller 1980), whereas northern habitats by mid-summer have large predictable supplies (Woodson 1954, Urquhart 1960, Borkin 1982). It is therefore possible that selection has shifted the monarch's larval developmental optimum to more moderate temperatures than its tropical congeners (Young 1982b), with the result that summer temperatures prevailing in the south may have become suboptimal or even lethal. Relative summer abundances of adults in the coastal plain, piedmont and mountains of Virginia (Clark and Clark 1951) are consistent with this view.

MAGNITUDE OF THE FALL MIGRATION AND NUMBERS OF GENERATIONS

Annual fluctuations of fall migrants have long been known (Scudder 1889), and Urquhart (1970) presented qualitative data suggesting a cycle in the annual abundance of North American monarchs which he hypothesized was caused by the buildup of a virus followed by the development of resistance in the monarch populations. An alternative explanation is that fluctuations result from variables affecting (1) survival rates in the overwintering colonies, (2) survival rates during the spring remigration and (3) the number of generations produced during the summer. The latter is thought to be latitudinally dependent with up to 5 broods in southern states and 1−2 in the north (Urquhart 1960, p. 175; Eanes and Koehn 1978). However, quantitative studies aimed at determining the numbers of broods relative to latitudinal, annual and climatic variables are lacking. As pointed out by Malcolm et al., (in preparation), an approach based on degree days using physiological development time, ***Asclepias*** availability and historical temperature data at various localities in the United States and Canada could be formulated to calculate the potential numbers of generations. These data could then be correlated with the historical record to see if in fact warmer years had larger fall migrations.

The problem is more complex than it appears: evidence suggests temporally staggered overlapping of generations which results both from successive breeding in situ and from adult immigration, presumably from more southern populations (Borkin 1982, Malcolm et al. in prep.). More generally, the total population of monarchs is undoubtedly a complex function of a dynamic equilibrium between northern breeding and southern overwintering (Morse 1980, Rappole and Warner 1980).

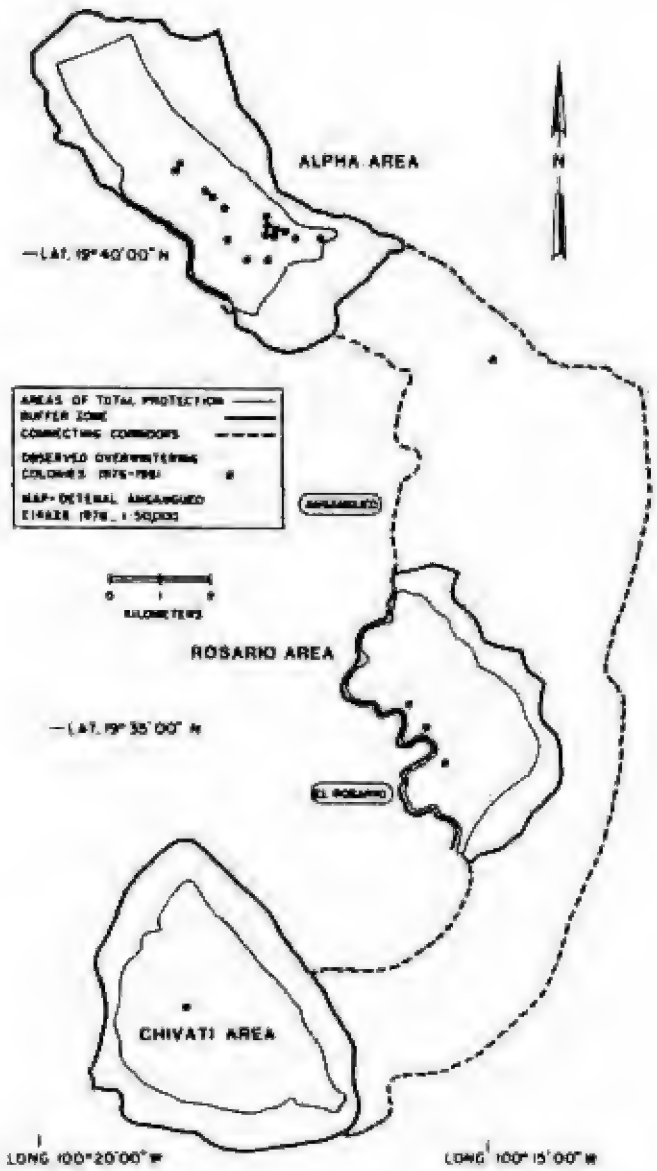


Figure 3

Map of three adjacent overwintering areas of the monarch butterfly in the Sierra Chincua (Alpha Area), in the Sierra el Campanario (Rosario Area) and on Cerro el Chivati (Chivati Area), in the state of Michoacán, Mexico. In each overwintering season from 1976–1981, the butterflies have occupied from one to several of the 21 sites (black dots) located by L. P. Brower and W. H. Calvert. The thin, thick and dotted lines are proposed conservation boundaries with suggested degrees of protection as indicated. This "Three Pearls Plan" has been submitted to The World Wildlife Fund, Pro Monarcha, A.C. and to various government agencies in Mexico. See text for further details.

CONSERVATION

Although the monarch ranges widely from North through Central and South America and westwards across the islands of the Pacific Ocean into Australia, and is not imperiled as a species, its North American migration and overwintering behavior is endangered as a unique biological phenomenon (Brower 1980; Anonymous 1982; Pyle 1983a,b; Calvert, Zuchowski and Brower 1984). Three reasons for this are: (1) deterioration of both milkweeds and nectar sources due to industrialized agriculture using broad spectrum herbicides (Berger 1978); (2) real estate development on overwintering sites in California (Anonymous 1983a, Jones 1983; Pyle 1983b; Lane 1984, 1985) and (3) degradation of the extremely limited fir forest ecosystems in Mexico through timbering and local fires. Mexico has had a long history of severe human impact upon its forests (Leopold 1950), and the destruction of overwintering habitats of temperate animals which migrate to the tropics is a worldwide problem

(Ripley 1980, Terborgh 1980, Ehrlich and Ehrlich 1981, Howe 1983).

Even high quality forestry practice degrades the Mexican overwintering habitat both by causing more butterflies to freeze (Calvert and Brower 1981; Calvert, Zuchowski and Brower 1982) and by allowing easier access to avian predators which kill up to 34,300 butterflies per day (Brower and Calvert, in press). If forest degradation results in smaller numbers of overwintering monarchs at these sites, mortality may increase because the intensity of bird predation is inversely proportional to colony size (Calvert, Hedrick and Brower 1979). Selective tree removal also lets more sunlight into the colony, butterfly activity increases and critical lipid reserves must diminish.

In cooperation with the World Wildlife Fund-U.S.A. and a Mexican conservation organization, Pro Monarcha A.C. (Anonymous 1982, Ortiz-Monasterio et al. 1980, Ogarrio 1984), we have worked with Federal planners in Mexico City and with Governor Cuauhtemoc Cardénas of Michoacán to develop and implement plans to protect one area of ***Abies religiosa*** forest (Brower and Calvert 1981, 1982; Anonymous 1983a,b; Pyle 1983a,b, 1984; Vásquez and Perez 1984) in the Angangueo region. Our plan for three adjacent major overwintering areas in the Sierra Chincua and Sierra El Campanario of Michoacán is shown in Figure 3 which includes protection of the ridges adjacent to the overwintering colonies where the initial fall aggregations occur, the upper stream valleys into which they coalesce and the lower stream drainages which serve both as refugia during times of extreme drought and as corridors for the spring remigration (Calvert and Brower, in preparation). Detailed examination of the boundaries and topographical concepts of the plan can be made by overlaying Figure 3 on the Angangueo 1:50,000 topographic map (Anonymous 1976).

Former President López Portillo (1980) issued a decree protecting the monarch per se (see also Urquhart and Urquhart 1980b); land acquisition to conserve the fir forest ecosystem is the essential next step. Increasing public awareness of the butterflies is resulting in tourist impact. The Government of Mexico needs to act quickly to assure the survival of one of the most remarkable of biological phenomena.

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MIGRATION STRATEGIES OF MONARCH BUTTERFLIES

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ABSTRACT

Vanishing bearings of 1599 individual monarch (*Danaus plexippus* (L.); Danaidae; Lepidoptera) butterflies were recorded in samples of $n \leq 20$ at various inland locations of the eastern United States as well as at coast lines parallel and nonparallel to the direction of migration. Due to the high degree of directionality of individuals, sample mean vector lengths are mostly near 1.0. The intersample variability is largely due to direct wind action i.e., drift in crosswinds and to indirect wind action i.e., the monarchs flying along the lee side of dunes, dams, wood margins, etc., even where this led them to deviate from the exact direction of migration. At the coast in unfavorable winds, including strong tailwinds, monarchs avoided heading out over the ocean. Butterflies took off repeatedly but returned after crossing the shore line. Inland, across the Piedmont plain as well as in the Apalachian Mountains, monarchs even migrated in strong tailwinds and very rapidly at altitudes at, and probably beyond, the range of powerful binoculars. Monarchs are probably able to keep track of and to compensate for displacements by wind. Overcast had no significant effect on headings or scatter. The mean directions summarized at two representative multi-sample inland locations (Blue Ridge and Ithaca) agree with the magnetoclinic direction predicted by Kiepenheuer's (1984) model of the magnetic compass.

INTRODUCTION

Insect migration is a widespread, sometimes spectacular phenomenon (e.g., Williams 1958, Johnson 1969, Baker 1978, Dingle 1978). However, despite much research and several books on the subject even the phenology of insect migration is, on the whole, less well understood than that of other migrants (Schmidt-Koenig 1975). With the exception of very large insects and economic pests such as locusts, most insect migrations are inconspicuous. Butterfly migration is often spectacular, but even so the phenology of migration, origin, destination, and mode of orientation of

migrating butterflies are as yet poorly understood. Among butterflies, the monarch ***Danaus plexippus*** ranks as the best studied long distance migrant inasmuch as its winter quarters have been located in California (Downes, in Williams, Cockbill, Gibbs and Downes 1942) and Mexico (Urquhart 1960, Brower 1977, Urquhart and Urquhart 1978). How the butterflies find their routes and destinations and how they navigate are, however, as yet entirely obscure.

In a number of publications, various aspects of the migration of the monarch butterfly have been discussed (e.g., Urquhart 1960, 1976; Urquhart and Urquhart 1978; Kanz 1977; Gibo and Pallett 1979). In a short communication (Schmidt-Koenig 1979) I reported on an initial series of observations of monarch migration. I was able to extend such observations considerably in the fall migration periods of 1978, 1980 and 1981. In addition to continuing to record data of inland migration, I particularly emphasized observations of migration under special circumstances such as at coast lines parallel and nonparallel to the general direction of migration, at tips of islands, at mountain ridges and under different meteorological conditions.

METHODS

Monarch migration is highly directional, each individual flying along a seemingly straight line. Vanishing bearings of migrants were, therefore, easily measured with a magnetic compass, allowing for the local declination. Monarchs migrating at low altitude within range of the naked eye (usually in headwinds or crosswinds) were tracked by eye until vanishing 50−100 m away, the distance depending upon color and brightness of the background. Monarchs migrating overhead beyond that range were tracked by 10 × 40 binoculars until vanishing. During large-scale migration, or high altitude migration requiring tracking with binoculars, I stayed in one location and tracked only those monarchs that passed overhead. During smaller scale migrations I positioned myself at a line roughly perpendicular to the direction of migration such as a road, a fence or the shore line, waited for a monarch to cross that line and walked to the crossing point to track the insect to the vanishing point. This eliminated parallax. Standard sample size was ≤ 20. Cloud cover, atmospheric visibility and visibility of the sun were noted. Surface wind direction was measured by tracking light objects thrown up into the air. Wind directions at higher altitudes were measured by tracking floating objects such as spider webs, whenever possible. Wind direction is given as is customary in meteorology, aviation and navigation. A 90° wind blows from due East. Wind strength was estimated on the basis of extensive prior personal experience with a hand-held wind meter. Samples were processed using the standard methods and statistical tests for circular data (Batschelet 1981).

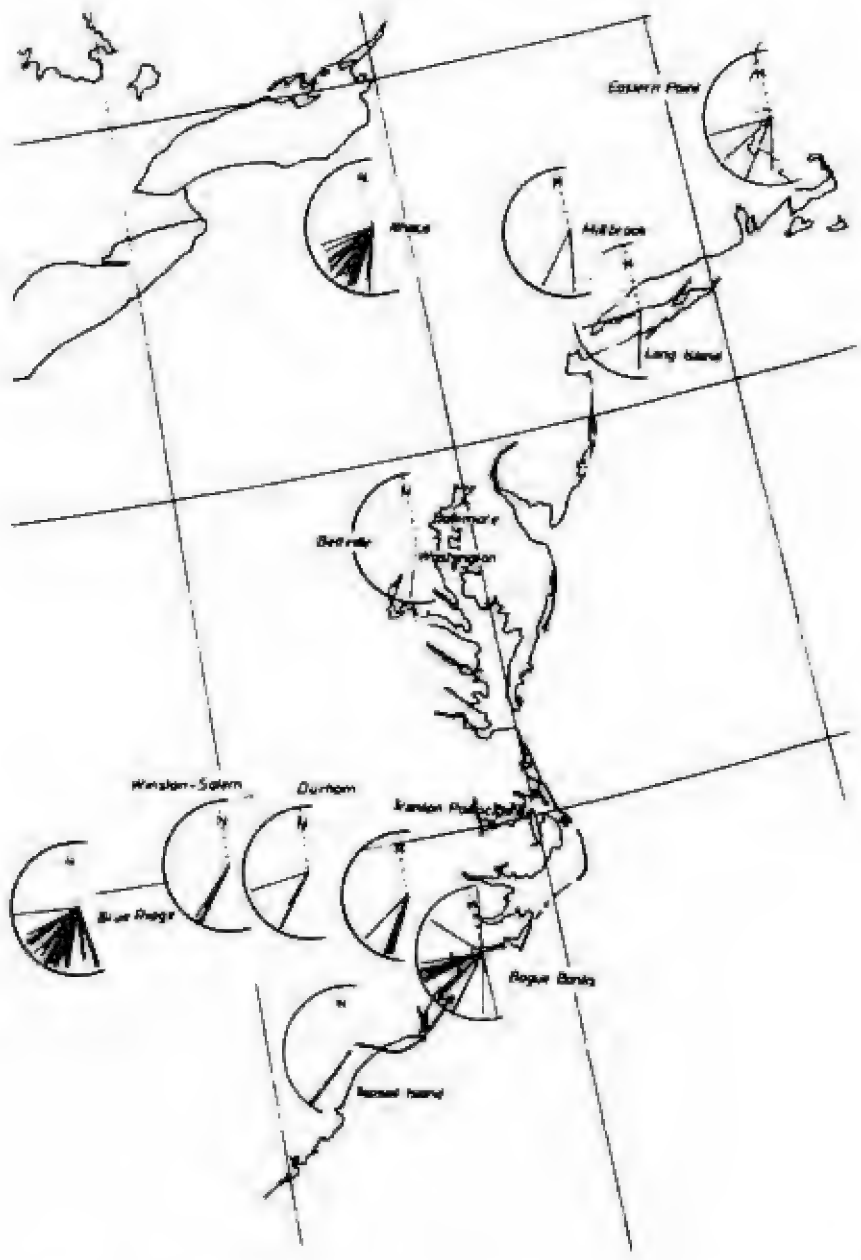

Figure 1

88 mean vectors of $n \leq 20$ monarchs vanishing bearings each obtained and summarized at the location indicated in the eastern United States during 4 fall migration periods. For more details see text, especially for the high proportion of westerly vectors at Bogue Banks; the north pointing vector is explained in Figure 3.

RESULTS

Figure 1 summarizes the mean vectors of 88 samples comprising 1599 individual vanishing bearings summarized at 11 locations and including those already given in Schmidt-Koenig (1979). Each sample represents a snapshot out of a stream of moving monarchs. Although the mean vectors are bunched at each location, even samples with vectors 10° apart may be significantly different from each other owing to the narrow range of individual monarch vanishing directions and correspondingly near unit-length vectors. Intersample variability is larger at Blue Ridge in a highly structured area than at Ithaca in much less structured terrain. This intersample variability is largely due to direct or indirect wind action. Direct wind action means that the butterflies are drifted by crosswinds. Indirect action means that in strong headwind or crosswinds the butterflies fly under the lee of suitable structures such as dams, wood margins, dunes, etc., even if they deviate from the general direction of

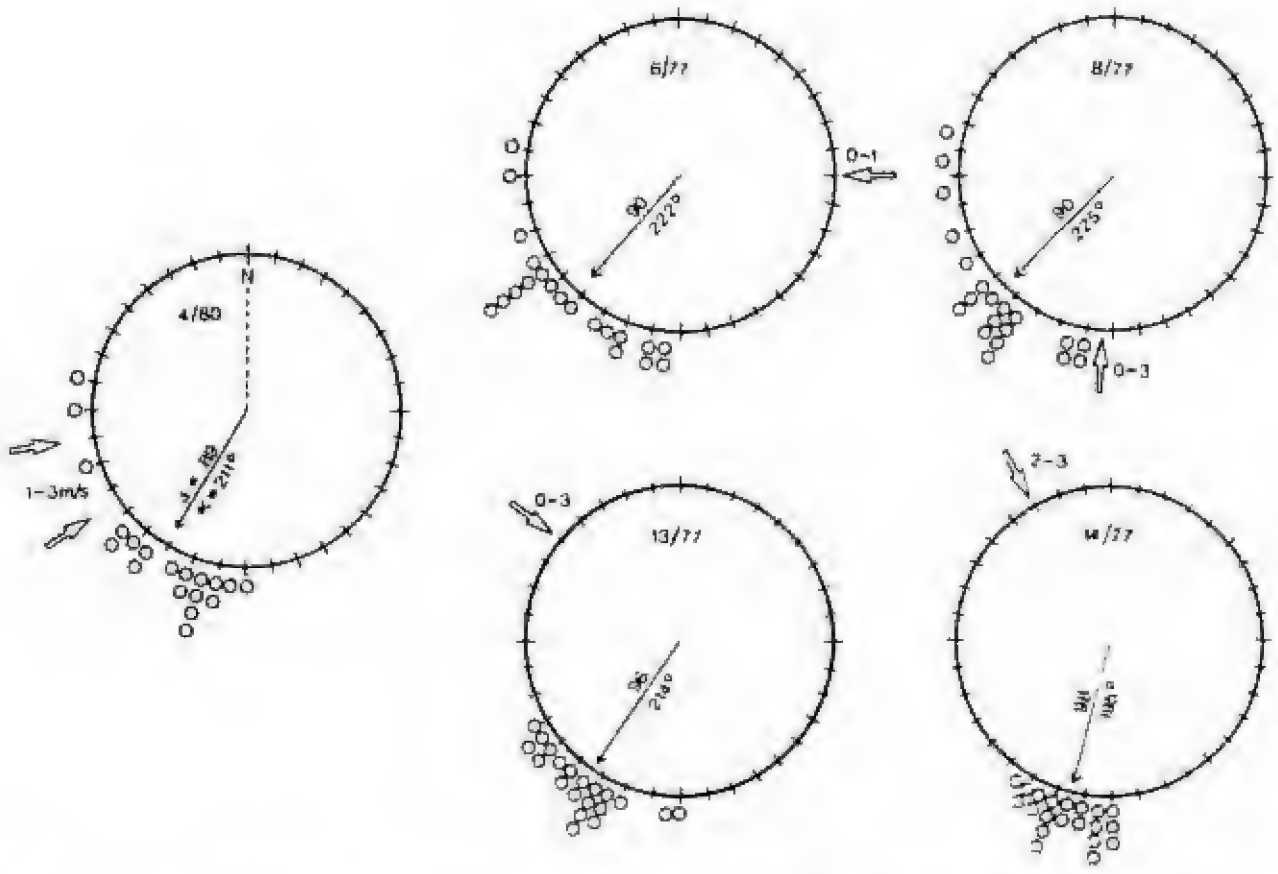

Figure 2

Five samples of 20 vanishing bearings each collected at Dodge Rd. near Ithaca, NY, under different conditions of light wind. The centripetal arrow at the periphery of each diagram indicates wind direction. Wind strength is given in $m \cdot s^{-1}$. Each open symbol at the periphery indicates an individual vanishing bearing. Mean vectors with direction and length and sample identification numbers are given; geographic north is given in sample 4/80.

migration.

Five samples were collected at the same location near Ithaca, NY, under a variety of light wind conditions. Some shift according to wind direction and strength is obvious in every sample (Fig 2), although the butterflies always visibly advance their headings to offset drift. The stronger the headwind or crosswinds, the lower the butterflies fly, and they fly under lee of dams, wood margins, dunes, etc., if necessary putting up with directions diverging from the general direction of migration rather than allowing themselves to be drifted e.g., out to sea. On Bogue Banks, NC, running roughly −80°, in southerly winds, monarchs migrated along the northern shore; in northerly winds they migrated along the southern shore or along inland wood margins. This behavior is the reason for the exceptionally large number of mean vectors pointing west at Bogue Banks in Figure 1. These data were collected during two fall migration periods and in wind directions ranging clockwise from 190° to 55°.

Monarchs do fly out over the ocean and cross major bodies of water under suitable wind conditions. I saw monarchs leave the southern shores or southern or western tips of Eastern Point, MA, Bogue Banks and Topsail Island, NC. I watched monarchs from boats over open waters, or arriving at the northern shore of Long Island, NY (Fig 1), or at the northern tip of Topsail Island, NC.

Monarchs are apparently able to assess the risk of heading out over the sea if the wind is unmanageable. This applies not only to headwind or crosswinds but also to strong tailwinds. For example in early October of 1980 at Bogue Banks, NC, large numbers of butterflies accumulated for days at the western tip of the island. Even on

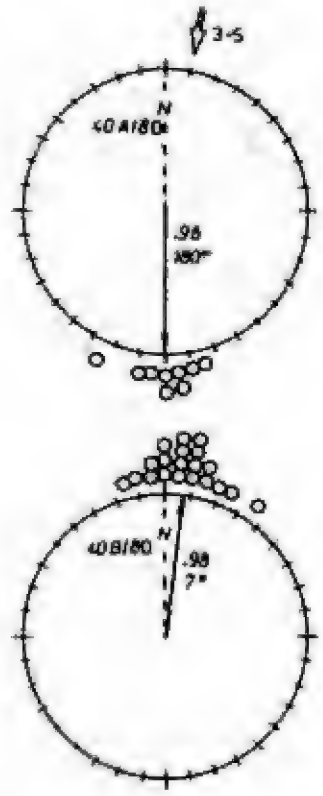

Figure 3

Two samples (symbols as in Fig 2) taken near the shore-line south of the western end of the dunes of Bogue Banks, NC, on 6 Oct 1980 during a strong northerly wind. Looking up into the sky (40A/80) I recorded monarchs that had taken off from behind the dunes. Looking down to the ground (40B/80) I recorded monarchs that had turned around and had dropped to the surface beating the wind back to the dunes.

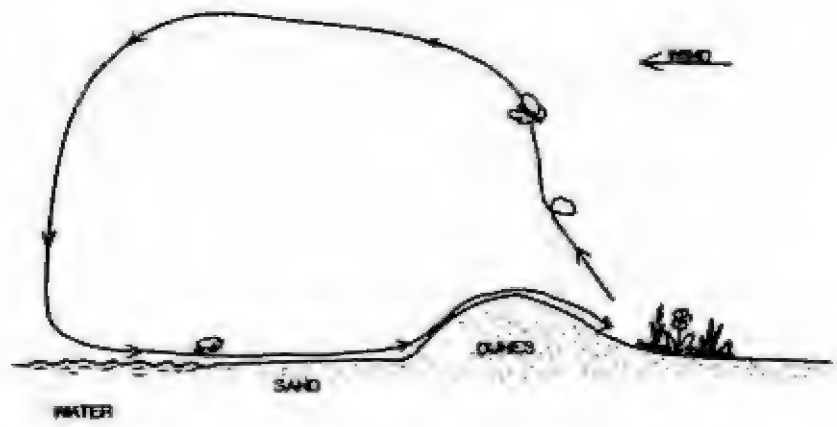

Figure 4

Diagrammatic sketch (not drawn to scale) of the observations made from 5 Oct into 7 Oct 1980 at the western tip of Bogue Banks, NC. For more details see text.

days with seemingly ideal tailwinds, 10° to 55°, 3 to 5 $m \cdot s^{-1}$ strong, and clear skies at the western end of the dunes of Bogue Banks or at the shore line, the butterflies appeared to leave the island but in fact could be seen returning close to the surface. I tracked monarchs that had taken off from the stands of golden rod (*Solidago* sp.) or sea-myrtle (*Baccharis halimifolia*) behind the dunes, heading in southerly directions, seemingly out to sea. However, I also tracked monarchs that had turned around, dropped to the surface and were beating the wind back to the dunes as low as possible over the surface of the water or sand. Samples 40A/80 and 40B/80 (Fig 3) were taken simultaneously, looking up and down, respectively. A continuous, cyclic process of monarchs taking off downwind but coming back low against the wind (Fig 4) went on

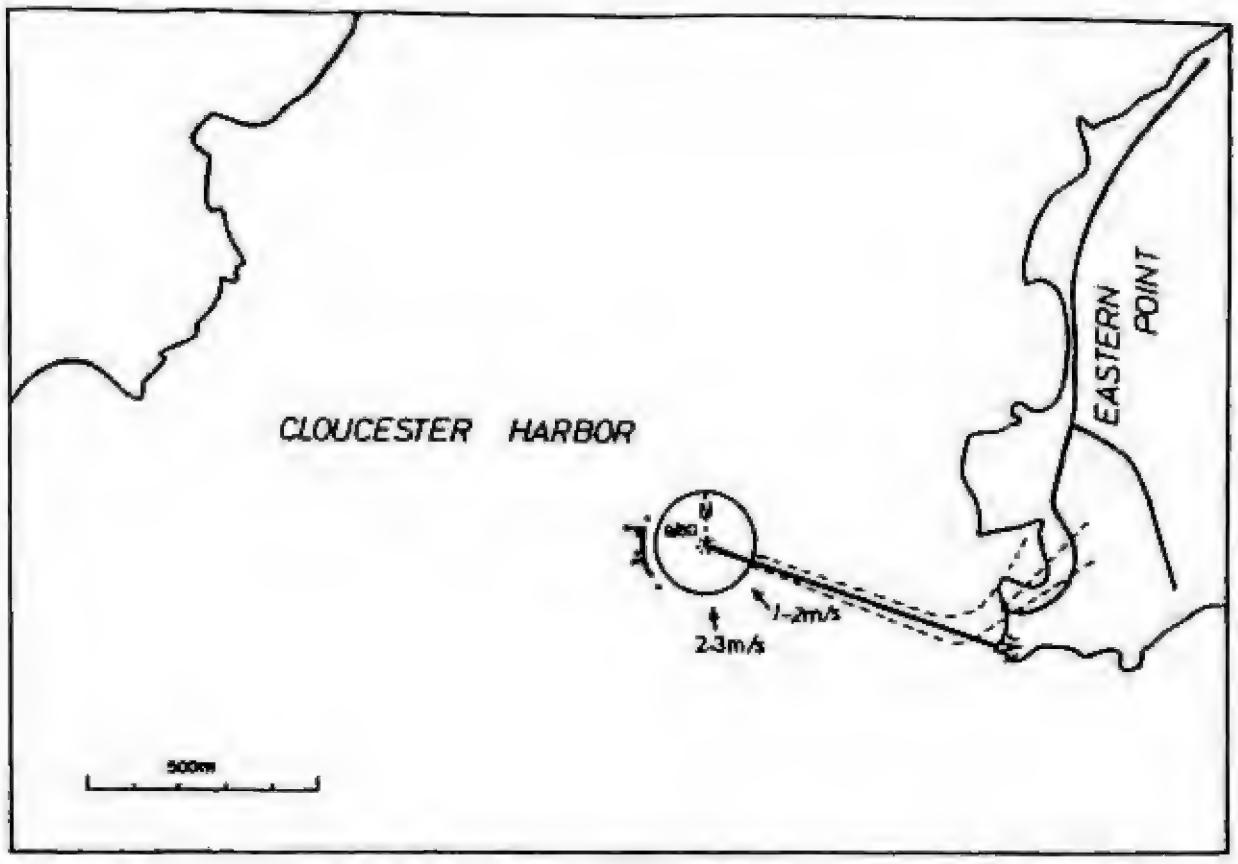

Figure 5

Migration at Eastern Point, MA, on 9 Sept 1980 in southeasterly winds and clear skies. Monarchs (dashed lines) approached the shore line near the ground then followed the breakwater (solid straight line pointing northwest). 18 vanishing bearings (black dots not drawn to scale) of butterflies heading out over the water were recorded at the light house at the tip of the breakwater. Geographic north and sample identification number are given inside the circle. The centripetal arrows at the periphery indicate wind direction. Wind strength is given in $m \cdot s^{-1}$.

from 5 Oct into 7 Oct 1980, with winds 10° to 55° and 3−5 $m \cdot s^{-1}$. A large proportion of monarchs turned around after having crossed the shore line on their way out to the sea. Some proportion was certainly blown out to sea. On 7 Oct 1980 I witnessed a calming of the 40° wind from around 5 $m \cdot s^{-1}$ to 1−2 $m \cdot s^{-1}$. Monarchs continued to take off towards south-southwest but no longer dropped down to the surface after having crossed the shore line to head back to the dunes. Within a short time the population of several thousand to ten thousand monarchs that had accumulated over several days had left the island. Such sequences of meteorological events at certain locations qualify as "migration traps" and may explain how the sometimes spectacular "clouds" of butterflies originate. The phenomenon could be called "meteorological synchronization."

On 9 Sept 1980 under clear skies, monarchs arrived at Eastern Point, MA, with southwesterly tracks low over sheltered land in southeasterly winds 1−3 $m \cdot s^{-1}$ (Fig 5). When encountering the shore line, they did not fly out to sea but changed headings by about 60° and flew under the shelter of a massive breakwater. At the end, however, they headed out over the water despite the prevailing crosswind of up to 3 $m \cdot s^{-1}$ that noticeably shifted the bearings clockwise to almost 270° from the standard south-southwest heading. In strong headwinds (205°−220° 6−11 $m \cdot s^{-1}$) a day later, monarchs accumulated at Eastern Point—another example of "meteorological synchronization." They were able to approach the buildings at the tip of Eastern Point under lee, tried over and over again to move on, but were blown

back inevitably when leaving the wind shadow.

The threshold at which monarchs consider wind conditions unmanageable must be a function of wind direction, wind strength, local conditions and possibly other variables. Many more data need to be collected before a fairly accurate assessment of that threshold can be made.

Eleven of the 13 samples given in Figure 1 at Trenton-Pollocksville, Durham (two at Durham are from 1977), and Winston-Salem were collected during a different kind of special meteorological condition between 9 Oct and 13 Oct 1981. During this period, fairly strong north to northeasterly winds (to 7 $m \cdot s^{-1}$) were blowing. While very few single monarchs could be seen near the ground, intense migration was going on at altitudes at least 300 to 400 m above the ground ("high altitude" migration) at which monarchs could be detected and tracked only by field glasses and often only against white clouds. In order to estimate migration across a large area, I collected samples along a line from the coast to a point just northwest of Winston-Salem ("NC transect") 9–13 Oct 1981. High altitude migration in following winds does go on much beyond the power of field glasses. Figure 6 shows samples taken near Grandfather Mt., NC, above about 1600 m elevation. Samples 27/80 and 28/80 were recorded overhead with field glasses, 31/80 at the same location without field glasses a day later with opposing winds forcing the monarchs to fly within 5 m of the ground and to exploit the lee area of obstacles. In the Colorado Rocky Mountains and in the California White Mountains, I watched several monarchs migrating above 3600 m altitude, again high up in tailwinds or calm conditions and close to the ground in headwinds or crosswinds.

DISCUSSION

Monarchs are not powerful flyers (e.g., Gibo and Pallett 1979) and are subject to considerable drift. Large-scale cross-country drifts must occur. Accumulations of butterflies at the Atlantic coast are probably the result of westerly winds. My data are as yet insufficient to confirm corresponding observations made in 1980 and 1981 when considerable numbers of monarchs showed up at the coast only during and after days with westerly winds. Likewise, I cannot as yet quantify the degree of deviation tolerated by migrants from the exact migration direction either by passive drift or as the result of active exploitation of lee sides of shelters. The small angular range of mean vectors in Figure 1 suggests a fairly low tolerance limit, the monarchs apparently preferring windward deviation to downwind drift. In order to successfully pinpoint their wintering grounds, the butterflies need to be able to keep track of and to compensate for displacements forced upon them by wind. I can present one "snapshot" out of a stream of migrating monarchs to support this notion. The samples shown in Figure 7 were taken on 7 Sept 1980 in fairly strong northwesterly winds at Tompkins County Airport, Ithaca, NY. Monarchs flying low in lee areas were more westerly directed after having crossed the airfield (6/80) and more southerly directed before having crossed it (7/80). They were certainly exposed to southeast drift while crossing the unsheltered airfield.

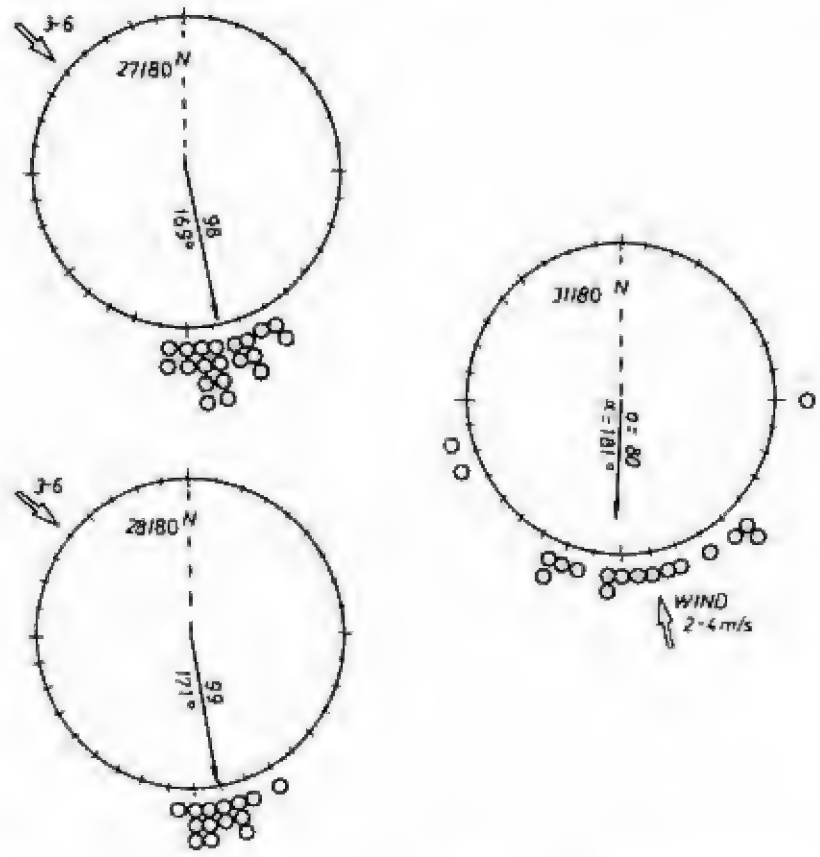

Figure 6

Three samples (symbols as in Fig 2) recorded near Grandfather Mountain, NC, above 1600 m elevation 26 and 27 Sept 1980, respectively. For more details see text.

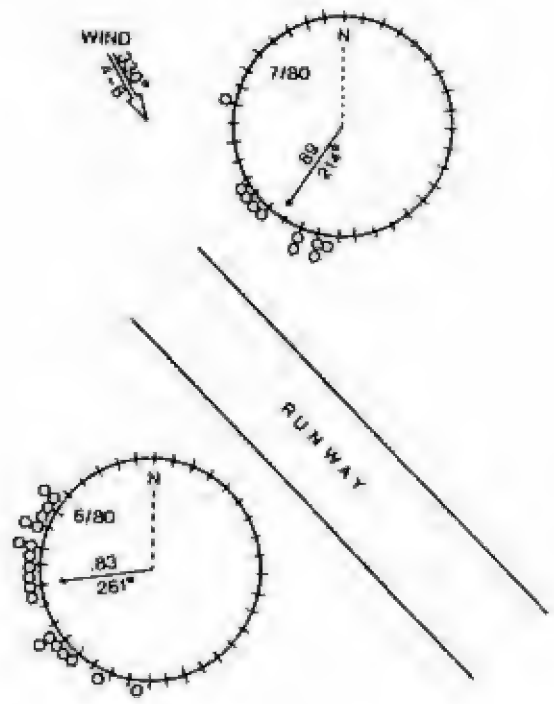

Figure 7

Two samples (symbols as in Fig 2) possibly demonstrating immediate compensation of drift. For more details see text.

A sun compass has been demonstrated in every animal, vertebrate or invertebrate, that has been tested. Standard experimental tests to demonstrate the use of the sun for compass orientation are those in which predictable shifts of direction can be obtained by using mirrors (e.g., Santschi 1911, Kramer 1951, von Frisch 1968) or upon clockshifts (e.g., Schmidt-Koenig 1960). In using mirrors the

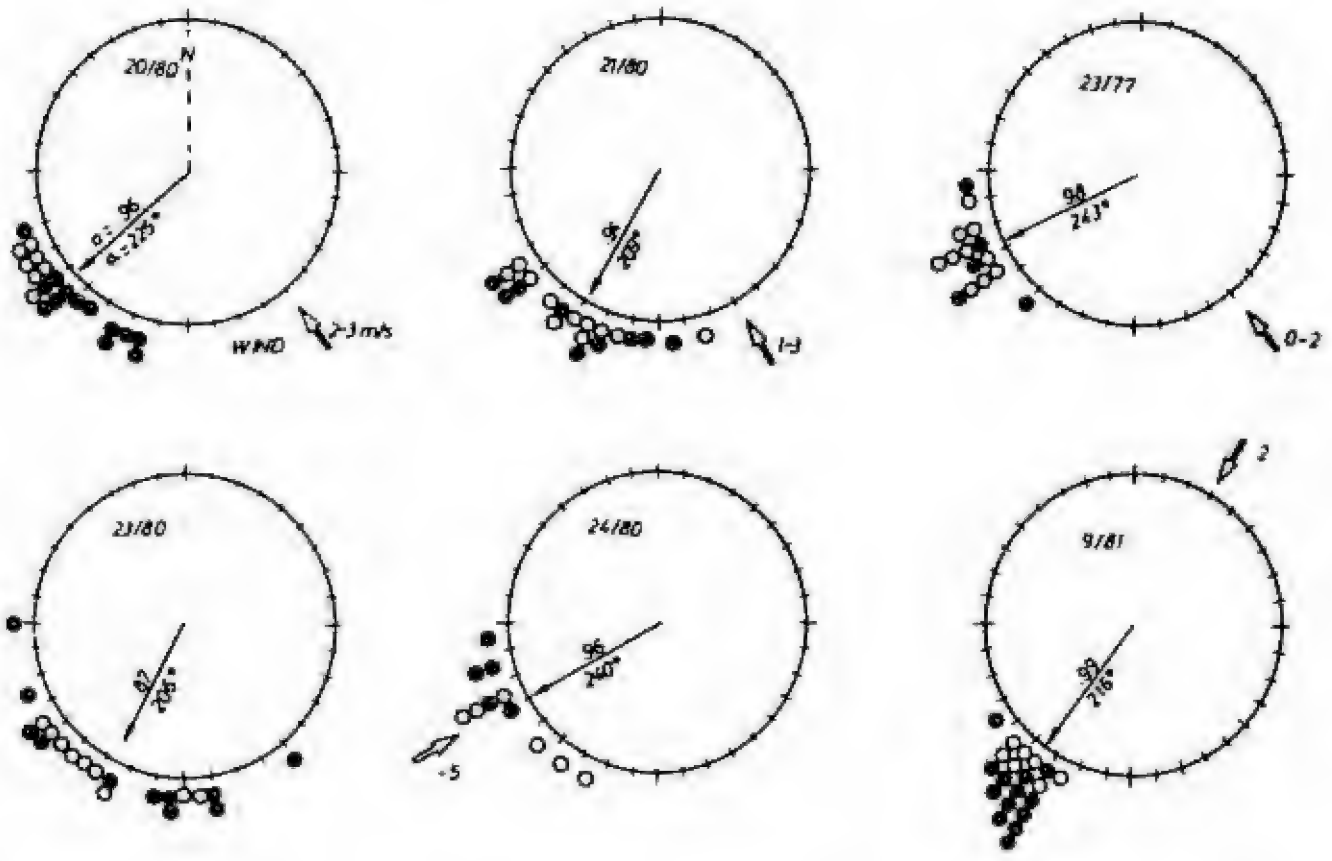

Figure 8

Six samples recorded partly under the sun (white symbols) partly under overcast (black symbols; otherwise symbols as in Fig 2) without simultaneous shift of wind direction. In sample 20/80, directions under sun and without sun are significantly different ($p < 0.01$; Watson U^2 test). There is no significant difference ($p < 0.05$; zame test) in any of the other samples nor in the summary of all six samples. Sample 24/80 was recorded at Black Mt. Gap, elevation 1450 m, near Mt. Mitchell, NC, partly in light rain and with clouds drifting across the gap in the opposite direction of monarch migration.

deviation accomplished corresponds to the angle subtended by the mirror. In clockshift experiments the deviation accomplished corresponds to the number of hours of time shift to which the animal and its internal clock, respectively, are subjected. The angular speed of the sun's azimuth being roughly 15° per h, a 6 h time shift produces roughly 90° of shift in direction. The experiments by Kanz (1977), therefore, do not disprove the use of a sun compass by monarchs. Kanz (1977) recorded the position of monarchs in opaque or transparent orientation cages under various sun conditions, unfortunately without experimental interferences which might have given more conclusive results.

If we extrapolate from findings on other insects (e.g., von Frisch 1968), as a first approximation we can assume that monarchs have a sun compass. Overcast skies, however, do not disorient migrating monarchs. Figure 8 shows 6 samples recorded under changing cloud conditions so that for one part of the sample the sun was visible (white symbols) but not for the other (black symbols). There was no obvious effect on the migrants. Likewise, 5 samples taken under complete overcast (Fig 9) give no indication of disorientation or other differences from samples recorded under sun. Thus if they have a sun compass, monarchs must have other means for orientation, possibly one based on the earth's magnetic field. Indeed, if one calculates (Table 1) the total mean vector for the two inland locations that may be considered fairly representative (because of large sample sizes and the absence of coast lines), the mean directions strikingly agree with the magnetoclinic headings calculated according

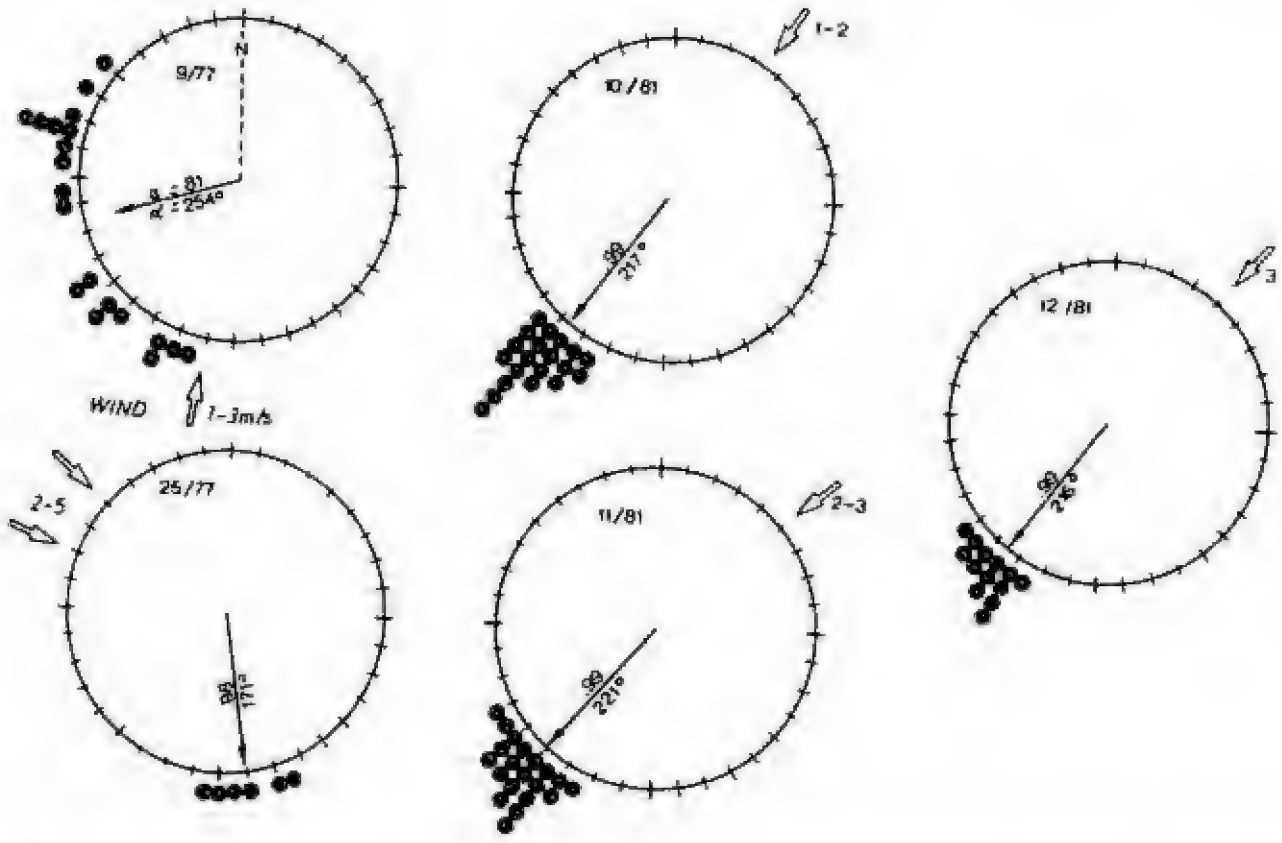

Figure 9

Five samples recorded under complete overcast (black symbols; otherwise symbols as in Fig 2). A thunderstorm approached and light rain began while 9/77 was being recorded. Monarchs were possibly heading for shelter in nearby woods west of my position. Heavy rain prematurely ended 25/77 after the sixth butterfly. Samples 10/81 through 12/81 represent high altitude migration recorded during the NC transect.

to Kiepenheuer's (1984) model of the magnetic compass under the assumption of a broad-front monarch migration parallel to that documented by Urquhart and Urquhart (1978) for the central eastern United States.

According to Kiepenheuer's (1984) model, magnetoclinic courses imply that the animal does not follow a specific course with respect to magnetic north ($\propto$m) but continuously maintains the same "subjective" angle of magnetic dip. This "subjective" angle of dip (γ') is the projection of the true dip (γ) on a plane vertical to the direction of the animal's long axis (direction of heading). Changing angles of true dip (e.g., when moving to southern latitudes) therefore result in changing course directions with respect to magnetic north. In the present case of the monarch butterfly, the mean direction of migration in the Ithaca area ($\gamma = 71°30'$, $\delta = -8°$) and in the Blue Ridge Mountain area ($\gamma = 67°00'$, $\delta = -4°$) changes by about 10°30′ to the south, but the same subjective angle of dip ($\gamma = 75°12'$) at both sites may be supposed to control this course. A course parallel to this with approximately the same γ' may be calculated from the data given by Urquhart and Urquhart (1978) for monarchs tagged in the Toronto area and in the Mexican winter quarters, respectively.

I tentatively conclude that monarchs use a magnetoclinic system similar to that suggested for birds by Kiepenheuer (1984). My tentative interpretation of the initial series of observations (Schmidt-Koenig 1979), that monarchs follow the great circle route, is no longer supported by the much more extensive data analyzed in the present paper.

Table 1

Geographical and statistical data of the two multisample inland summaries Ithaca and Blue Ridge (Fig 1). n = total number of individual vanishing bearings; $\bar{\alpha}_n$ = total mean vector of n vanishing bearings; $C_{99\%}$ = 99% confidence interval of $\bar{\alpha}_n$; α_M magnetoclinic heading according to Kiepenheuer (1984).

		n	$\bar{\alpha}_n$	$C_{99\%}$	α_M
Ithaca	42°30′N; 76°30′W	348	224°03′	± 4°40′	224°
Blue Ridge	36°00′N; 82°00′W	486	214°42′	± 3°51′	214°

My observations fully confirm and support those made by Gibo and Pallett (1979) on flying strategies during migration. These authors report observations similar to mine as to the effect of wind direction and strength on initiation or discontinuation of migration, on altitude of flight, the use of wind shadow, and the flying techniques used in crossing obstacles. I can particularly confirm the observations on the use of thermals. Many times I observed monarchs soaring past at high speed in tailwinds immediately beginning to circle when they encountered thermal lift such as that originating from black surfaces of parking lots. In calm conditions or light winds with a tail component, I frequently observed, as did Gibo and Pallett (1979), monarchs circling out of sight in thermals overhead, sometimes together with hawks such as ***Buteo platypterus***. I agree with Gibo and Pallett (1979) that monarch butterflies are highly adapted to exploit meteorological conditions to save energy. According to these authors, monarchs utilizing all strategies have more than enough resources to fly to their wintering grounds in Mexico. Without these adaptive strategies the monarchs would have to spend much more time migrating, possibly at the expense of one reproductive generation in late summer. Most amazing of all is, however, that the monarchs' highly flexible migration strategies mentioned above are accomplished each fall by a population of entirely naive animals.

Our observations (Gibo and Pallett 1979, Schmidt-Koenig 1979 and herein) are relevant to the questions raised by Walker and Riordan (1981) who discuss contributions by Williams (1958), Johnson (1969) and Baker (1978). Monarch butterflies seem to determine their direction of migration directly—possibly using the geomagnetic field according to the Kiepenheuer (1984) model. However, they also rely on favorable wind as a major means of transport even at high altitudes, high velocities and presumably for long distances.

ACKNOWLEDGMENTS

I am grateful to J. Kiepenheuer, Tübingen, for calculating the magnetoclinic heading, to him and to P.H. Klopfer, Durham, NC, for critically reading and improving the manuscript.

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HORMONALLY MEDIATED EVENTS IN ADULT MONARCH BUTTERFLIES

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ABSTRACT

At least three hormones are indicated in adult monarch (*Danaus plexippus*) butterflies. The juvenile hormone clearly plays a critical role in the regulation of ovarian growth, male and female reproductive gland development and diapause; it also seems to be important in the regulation of aging, migration and male reproductive behavior. Hemolymph juvenile hormone levels are predictably variable during the adult annual cycle, with the highest and lowest values generally found in prediapause and postdiapause adults, respectively. Juvenile hormone titers may be diminished by the action of a specific esterase that is optimally active at thoracic temperatures generated during flight. Males are more sensitive to juvenile hormone than are females. Two additional hormones, both apparently peptides, also seem to play important roles during the annual adult cycle of this species. A diuretic hormone is principally responsible for the pronounced diuresis occurring immediately after eclosion. An adipokinetic hormone, biologically and chemically similar to hormones found in shrimp and locusts, appears to be the principal agent acting to mobilize stored lipid during flight. Both hormones are present in all stages of the adult cycle. Comparable endocrine mechanisms are indicated in the painted lady *Vanessa cardui* and in the mourning cloak *Nymphalis antiopa*.

INTRODUCTION AND METHODS

In the early 1970's I became interested in the neuroendocrinology of adult lepidopterans. My interest in this subject was stimulated by the absence, at that time, of any detailed information dealing with hormonal regulation in adults of that order, and by my opinion that the adult stage of such a large and important taxon should not be neglected by endocrine physiologists. My attempts to identify a suitable species for endocrine studies on adult lepidopterans soon focused on the monarch butterfly *Danaus plexippus*. There were several reasons for selecting this species: (1) monarchs are large enough for a variety of physiological manipulations to be rather easily performed; (2) the species is plentiful in our area from late May to early September, and it can be easily reared in large numbers during that period; (3) adult monarchs can be routinely obtained from the overwintering sites in California at regular intervals

throughout the winter; and (4) monarchs were known to be migratory and to exhibit reproductive cycles, suggesting the probable existence of hormonal systems. Against that background, my collaborators and I have examined adult monarchs of both sexes in an attempt to discover at least some of the specific endocrine events that might occur in this species. We have hoped that such studies would not only yield data on monarchs but also provide some basis for future generalizations concerning the neuroendocrinology of both adult lepidopterans and adults of other holometabolic insect orders. We have also proceeded under the assumption that data concerning the neuroendocrinology of monarchs might eventually contribute to the development of economically and ecologically sound insect control strategies based upon the artificial manipulation of vital endocrine mechanisms.

During the past decade my collaborators and I have shown that juvenile hormone plays a very important role in a variety of monarch activities, and we have also obtained evidence for the existence of at least two additional hormones being used by adults of this species. In this report I will review our past and present studies with monarchs, and I will summarize our current understanding of the importance of hormones during the annual adult cycle of this species. I see this paper as dealing with the monarch cycle in four ways: (1) preparation for migration, (2) characteristics of migrants (3) changes after completion of migration and (4) differences between northbound and southbound migrants, as summarized in the final figure.

Our research has been conducted on adult insects reared or captured in the Minneapolis, Minnesota area from late May to September, and also on adults shipped to us from California during October through March. Thus we are examining eastern monarchs in summer and western monarchs in winter. Additional research (now in progress) is required to determine what similarities and/or differences exist between these animals and western summer, and eastern winter adults of this species. The specific manipulations performed during our studies are adequately described in the references listed below. Unless otherwise indicated, all data in this report are presented as mean ± s.e.m.

RESULTS

Posteclosion Growth of the Reproductive Tract

Several of our investigations have dealt with the regulation of reproductive tract growth after eclosion of summer resident males and females (Barker and Herman 1973, 1976; Herman 1975, 1982; Herman, Lessman and Johnson 1981). These studies, summarized in Table 1, show that conspicuous growth normally occurs in most male and female reproductive organs during the first few days after eclosion. A variety of experiments, some of which are presented in Table 1, indicate that juvenile hormone (JH) is responsible for stimulation of this rapid posteclosion growth in the female ovaries, colleterial glands, receptacle glands and bursae copulatrix and in the male accessory glands, tubular glands and ejaculatory ducts. (For convenience, only our ovarian and ejaculatory duct data are presented in Table 1 and elsewhere in this

Table 1
Effect of juvenile hormone on monarch reproductive organs.

	Wet Weight (mg)	
	Ovary	Ejaculatory Duct
Intact adults		
At eclosion	1.9 ± 0.1	2.1 ± 0.1
5 days posteclosion	34.0 ± 2.4	14.3 ± 0.5
Allatectomy		
Allatectomy only	1.8 ± 0.3	1.9 ± 0.3
Allalectomy + Solvent	2.1 ± 0.2	2.3 ± 0.2
Allalectomy + 10.0μgJH I	17.6 ± 1.3	10.4 ± 0.8
Sham-operated	26.4 ± 3.2	11.9 ± 1.2
Neck ligation		
Ligation only	2.0 ± 0.2	2.1 ± 0.2
Ligation + solvent	2.2 ± 0.2	2.0 ± 0.2
Ligation + 0.1μg JH II	2.1 ± 0.2	5.2 ± 0.7
Ligation + 1.0μg JH II	2.6 ± 0.3	7.7 ± 0.7
Ligation + 10.0μg JH II	9.3 ± 0.6	12.0 ± 0.7
Ligation + 100.0μgJH II	18.2 ± 1.5	16.4 ± 0.5

Mean n = 12.4; all animals reared in June−July in MN; all posteclosion animals held 5 days in summer conditions (25°C and 16 hour photophase).

report, but such data are representative of the events occurring in other JH-sensitive male and female organs.) In our experiments, allatectomy or neck ligation prevents growth of the above organs, while injections of JH into animals so treated result in pronounced, dose-related growth. These kinds of experiments have also shown that both JH I and JH II are effective in each monarch sex, but that JH III has little effect in either sex (Lessman, Rollins and Herman 1982). As indicated in Table 1, male monarchs may be more sensitive to JH, since doses of 0.1 and 1.0 μg JH II, that are ineffective in ligated females, result in significant enlargement of male JH-sensitive organs, e.g., the ejaculatory duct.

In addition to the studies outlined above, we have also used the *Galleria* bioassay to determine the amount of JH activity present in adult monarch hemolymph during the posteclosion period (Herman et al. 1981). Our assays showed high levels of JH activity during the first few days of posteclosion life in insects of both sexes, when reproductive tract growth is generally accelerated, and low levels of such activity from 8−30 days posteclosion when tract growth is very much reduced (see Table 2). Our data on JH titers also indicate sexual differences in JH production in posteclosion monarchs; i.e., females exhibit a peak of JH activity averaging over 10^6 *Galleria* units·ml^{-1} hemolymph on the third day after emergence, but no such peak occurs in

Table 2

Hemolymph titers of juvenile hormone in adult monarch butterflies.

	Galleria Units/ml Hemolymph		
	Male	Female	Both Sexes
Posteclosion			
Day 0–6	2.8×10^5 (23)	3.9×10^5 (23)	–
Day 8–30	3.8×10^3 (18)	1.4×10^3 (22)	–
Wild-Caught			
June–July	–	–	1.4×10^5 (15)
August–October	–	–	3.3×10^3 (29)
November–January	–	–	2.1×10^2 (27)
February	1.3×10^6 (5)	1.3×10^2 (5)	–

n in ( ) is number of assays of pooled hemolymph samples; data from Herman et al. (1981) and Lessman and Herman (1983).

males (Herman et al. 1981).

To date we know little about the molecular or biochemical events associated with JH action in the post eclosion monarch. However, Pan and Wyatt (1971, 1976) have demonstrated that JH regulates vitellogenin production in this species, and Herman and Peng (1976) have reported JH stimulation of an apparent peptide from the ejaculatory duct that acts as a sperm activator. In addition, monarchs apparently possess both a JH binding protein an a JH-specific esterase (Lessman and Herman 1984). Since the esterase is maximally active at temperatures approximating those found internally in flying monarchs, it is possible that flight activity may act indirectly to lower hemolymph titers of JH (Lessman and Herman 1981).

Reproductive Tract Development During the Annual Adult Cycle

We have also examined the condition of the male and female reproductive tracts at intervals throughout the year. This research is summarized in Figure 1, which again presents only our data for ovarian and ejaculatory duct wet weights.

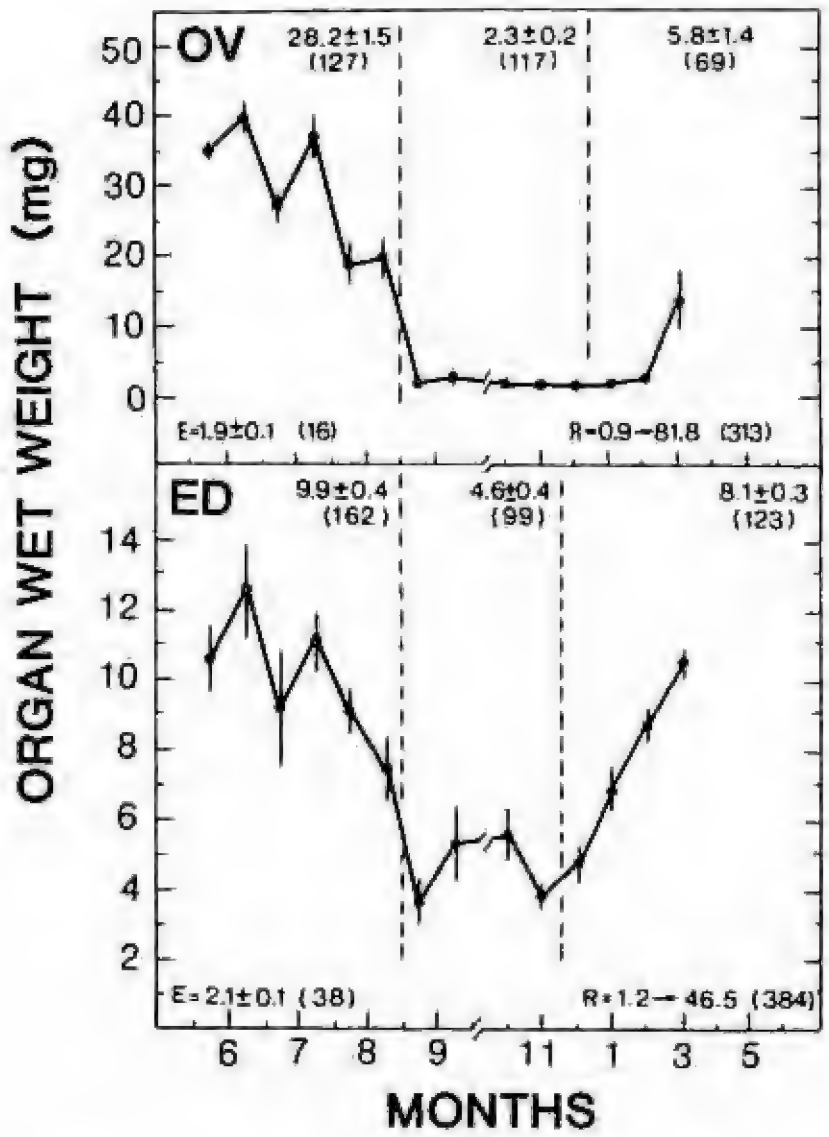

Figure 1

Developmental changes in female and male JH-sensitive organs during the annual adult cycle, as indicated by changes in the ovary (OV) and ejaculatory duct (ED), respectively. Dashed vertical lines indicate the diapause period (see text); E = organ wet weight at eclosion; R = range of weights observed; n in ( ); broken line separates Minnesota and California monarchs; methods described in Herman (1975) and Herman et al. (1981).

As shown in Figure 1, the JH-sensitive organs of wild-caught males and females were most well-developed from late May to early August. In late August collections of premigratory adults, however, there was an abrupt decline in the size of such organs. In late August females the relevant organs generally showed no development past the eclosion condition, and they remained in that state until late February or early March. By contrast, the male ejaculatory duct did grow in late August through December, to about twice its eclosion value, and it also exhibited pronounced growth from January through March, a period in which the mean value for ejaculatory duct weight was comparable to that found in May through August. Thus although both tracts exhibited reduced growth during the post-August period, the male tract was generally more well developed (relative to the eclosion value), and renewed growth of the male tract occurred sooner than in females. Injection of JH into either sex from late August to March resulted in prompt and conspicuous growth of the JH-sensitive male and female organs (Herman 1973, 1975).

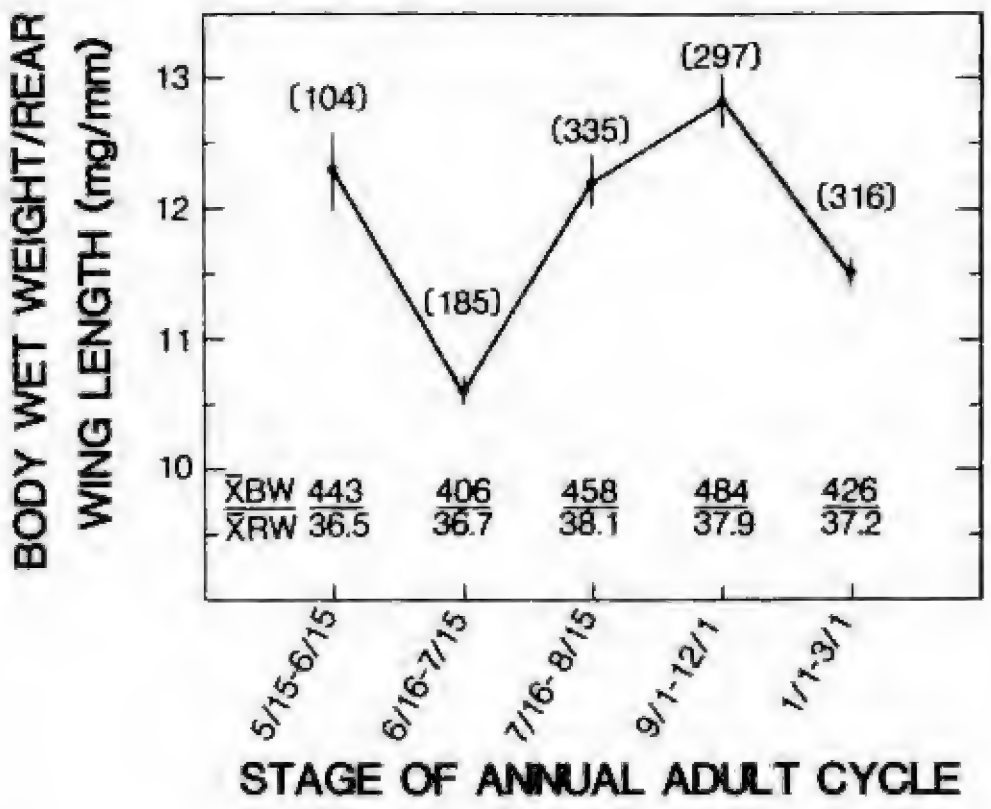

Figure 2

Changes in body weights and rear wing lengths of adult monarch butterflies during the annual adult cycle. Male and female data combined; BW = whole body wet weight and RW = rear wing maximal length; n in ( ); all animals wild-caught.

We have also determined total body wet weights and maximum length of rear wings of male and female monarchs captured at intervals during the annual adult cycle. These data are summarized in Figure 2, which presents our mean values and the mean body weight/rear wing length ratios at selected intervals during the year. Immigrants to Minnesota in late May and early June were characterized by relatively high values, but these ratios dropped precipitously as the aging immigrant population lost body weight, while wing dimensions remained constant, in late June and early July. Ratios rose sharply in late July and early August, when the majority of the resident population consisted of young adults, with high body weights and significantly larger wings, that had emerged in Minnesota. The highest mean ratios were observed from late August to December in both Minnesota and California populations, when both body weights and wing lengths were high. Declining body weight during the remainder of the overwintering period was the major cause of the decreased ratios seen in January through March.

Table 2 also summarizes our assays of JH activity in pooled hemolymph samples from monarchs collected at specific times of the annual cycle (Lessman and Herman 1983). During the period of peak reproductive activity (i.e., June and July) the monarchs of Minnesota had hemolymph JH titers comparable to those seen in young posteclosion insects. The reduced development of the male and female JH-sensitive organs seen in wild-caught individuals (i.e., migratory adults) from late August to October was accompanied by a decline in JH activity of about two orders of magnitude. In subsequent months, JH levels remained low in both sexes, with the

exception of a striking increase of JH activity in hemolymph from males sampled in February. When the JH titer data are considered along with the reproductive organ wet weights in Figure 1, it appears that the low levels of JH activity present in migratory adults from late August through October are sufficient to stimulate some development of sensitive male organs but not sufficient to cause noticeable growth in comparable female organs. In addition, the enhanced reduction of JH seen in February males seems to be at least partially responsible for the pronounced enlargement of the JH-sensitive male organs seen at that time.

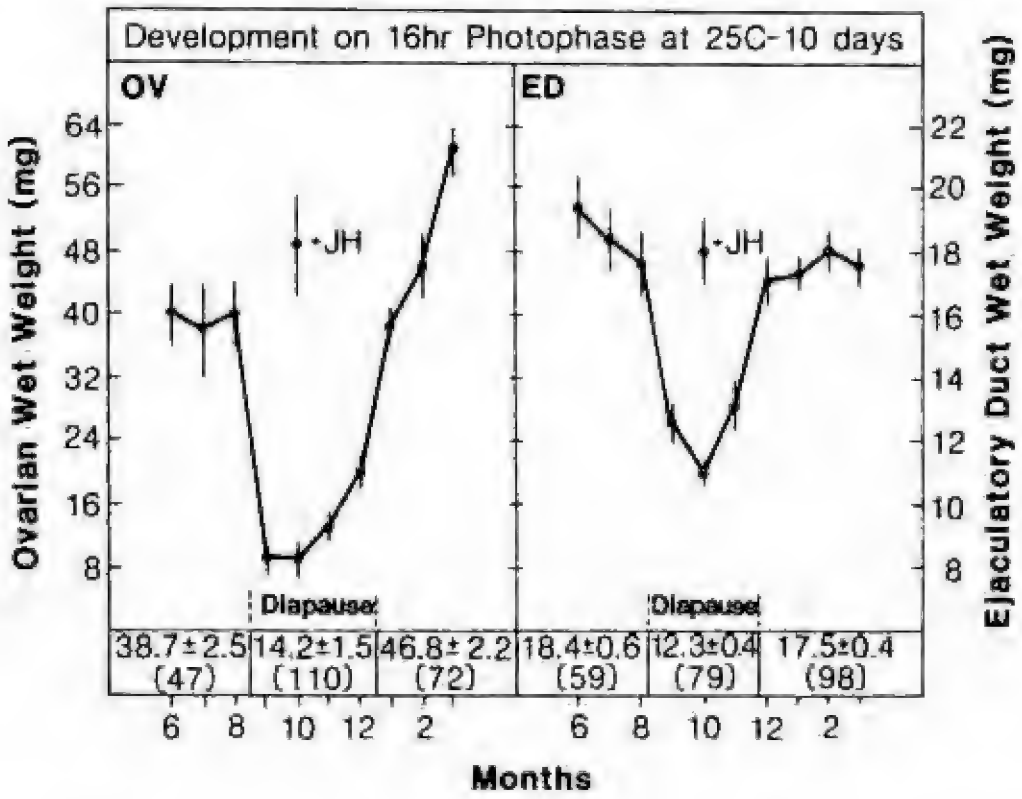

Figure 3

Demonstration of adult diapause in monarch butterflies. OV and ED as in Figure 1; n in ( ); data from Herman (1981).

Adult Reproductive Diapause

Other investigations in my laboratory have dealt with the phenomenon of diapause in this species (Herman 1981). For these studies we have placed monarchs on the day of eclosion in June—early August, or at the time of capture in September—March, in incubators programmed for summer conditions, and determined the growth of the pertinent organs in response to this treatment. As shown in Figure 3, both male and female tracts exhibited a period of reduced response, i.e., diapause, lasting from September to December (males) or January (females). During diapause JH-sensitive organs did not grow as rapidly as they did from June—August or from the end of diapause until the colonies dispersed. If diapause animals were injected with 10 μg JH I, they exhibited reproductive growth comparable to that found in nondiapause animals (see Fig 3). These studies allowed us to define three major stages in the adult monarch annual cycle, i.e., prediapause, diapause and postdiapause. Only in the former and

Table 3
Effects of juvenile hormone on monarch longevity.

	Survival in Summer Conditions			
	Males	*n*	Females	*n*
Life cycle stage				
Prediapause	41.8 ± 2.0	38	41.3 ± 2.5	43
Diapause	44.4 ± 3.1	39	64.1 ± 2.9	56
Postdiapause	28.1 ± 1.8	109	39.4 ± 2.0	86
Allatectomy				
Sham controls	43.7 ± 4.2	12	42.5 ± 2.6	21
Allatectomized	63.4 ± 7.4	8	63.9 ± 6.4	17
JH injections				
Controls	30.8 ± 3.0	45	43.0 ± 3.0	41
Five AJH injections	19.4 ± 2.0	35	24.4 ± 1.5	70

30–300 μg AJH injected on alternate days for 10 days; controls injected with JH vehicle; summer conditions are 25°C on a 16 hour photophase; all animals fed 30% honey on alternate days; allatectomies performed on prediapause adults, and JH injections performed on post-diapause adults.

later stages are monarch adults capable of responding to summer conditions with rapid growth of JH-sensitive reproductive organs. There does appear to be a sexual difference with regard to diapause in that female tract development is more restricted and female diapause lasts longer than that of males (see Fig 3). In addition, postdiapause females, which were frequently mated, exhibited a higher level of JH-sensitive organ development than did our prediapause females which were all virgin. This difference is apparently due to the stimulatory effects of mating in females of this species (Herman and Barker 1977).

Adult Senescence

We have also examined the role of JH in aging in adult monarchs. These studies were prompted by our observations of relatively large numbers of old monarchs, i.e., those with low body weights and badly faded and battered wings, in summer populations, but few such animals were found in collections from the overwintering colonies. Since senescent monarchs were most common in summer when JH levels were high, and least common when JH levels were known to be diminished (diapause and postdiapause), we examined the possible role of JH in monarch aging.

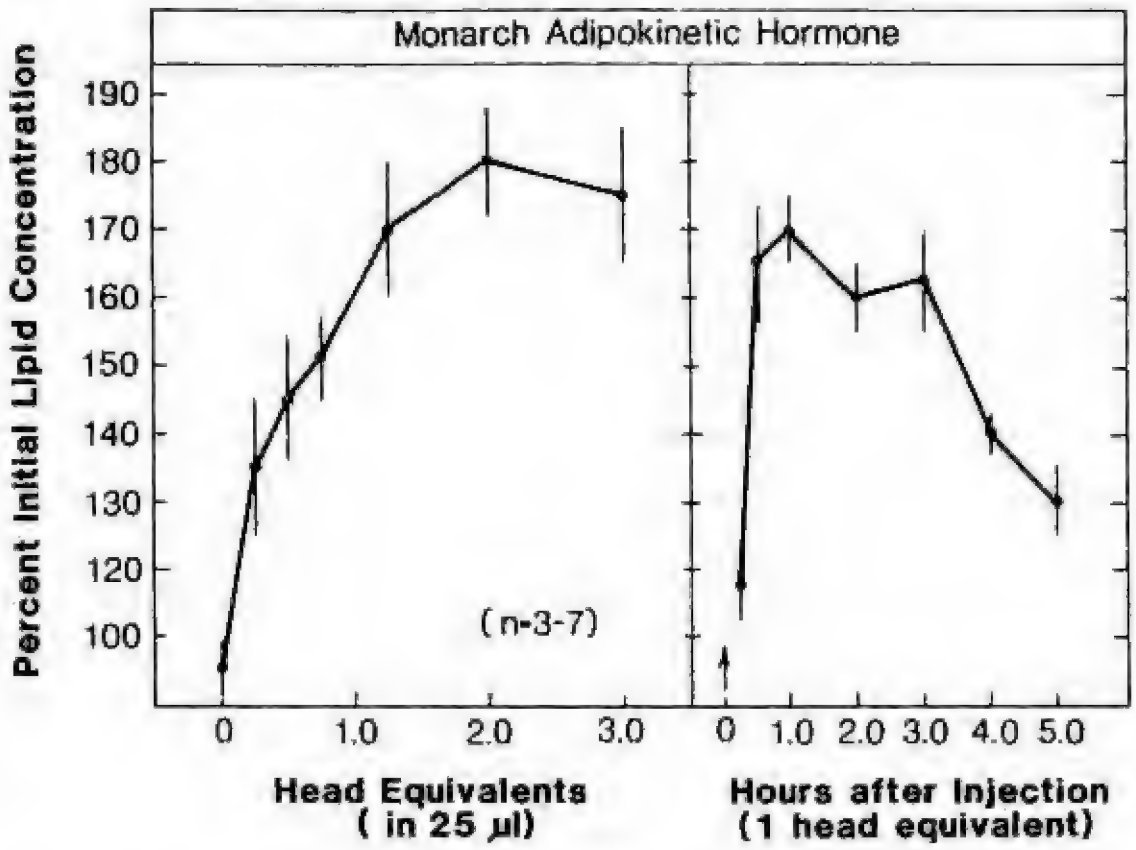

Figure 4

Effects of head extracts on hemolymph lipid levels in adult monarch butterflies. Left, relationship of dose injected to response obtained; right, changes in hemolymph lipid with time after injection; data from Dallmann and Herman (1978).

Indirect evidence for JH involvement in aging of this species came from experiments dealing with the longevity of monarchs from different stages of the annual cycle. In these studies males and females were held in summer conditions from the day of emergence (prediapause) or capture (diapause and postdiapause) until the day of death. Both pre- and post-diapause females survived for about 6 weeks in such conditions, but diapause females lived for about 10 weeks (see Table 3). Thus female longevity was shortest when JH levels were known to be high, as indicated by JH titers and/or growth of JH-sensitive organs. Again, males exhibited a different pattern. Males in diapause showed no significant increase in longevity over prediapause males, and males in postdiapause only lived for about 4 weeks. These male differences could be due to enhanced male sensitivity to JH (see Table 1 and Fig 1) and increased JH production by postdiapause males (see Table 2). Direct evidence for a role of JH in monarch senescence came from ablation/replacement experiments such as those summarized in Table 3. Allatectomy of prediapause males and females resulted in enhanced survival of both sexes, while sham-operated control insects lived for the same time as intact prediapause controls. In addition, injections of multiple doses of material with high JH activity (the Ayerst mixture of JH I isomers or AJH) decreased survival time in both sexes. Therefore we possess both indirect and direct evidence that monarch longevity is at least partially determined by the effective titer of JH; high JH titers seem to stimulate both reproduction and rapid aging, while low titers of JH result in low levels of both processes.

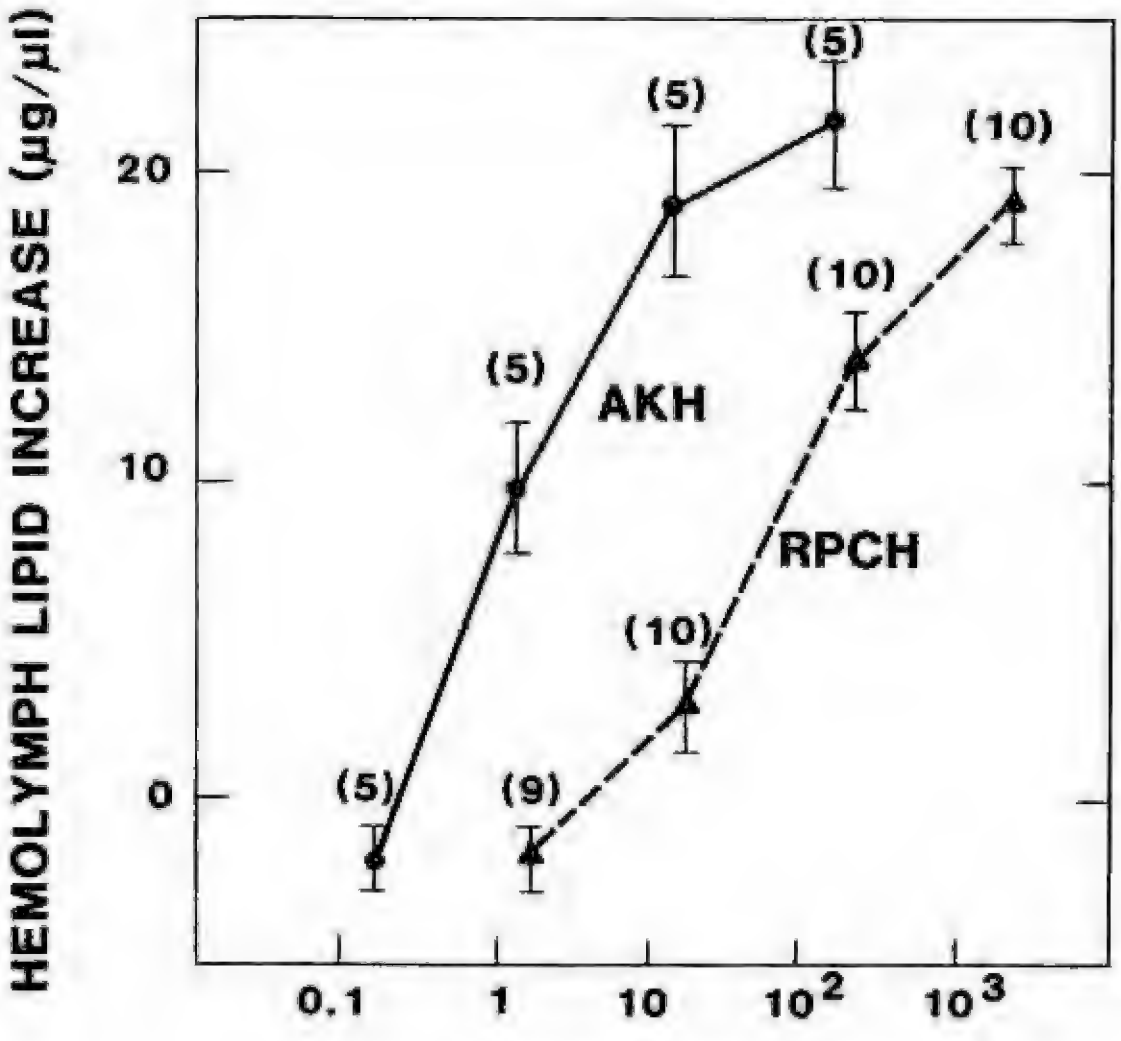

Figure 5

Effects of synthetic locust AKH and shrimp RPCH on hemolymph lipid levels in diapause monarch adults. Data from Dallmann et al. (1981); n in ( ).

Monarch Adipokinetic Hormone

Our collaborations in Denmark led to the demonstration of shrimp red pigment-concentrating hormone (RPCH) activity in the heads of monarch butterflies (Herman, Carlsen, Christiansen and Josefsson 1977). Subsequently, it became apparent that comparable activity in the locust corpora cardiaca was due to the similarity of locust adipokinetic hormone (AKH) to shrimp RPCH (Mordue and Stone 1976). The existence of RPCH-like activity in monarch heads suggested that monarchs might use the active substance to regulate lipid levels in the hemolymph. Experiments designed to examine this possibility are illustrated in Figure 4, where some of our data supporting the existence of a monarch AKH are presented.

In our studies the monarch AKH appears to be a peptide acting to mobilize diglycerides from the fat body during periods of flight (Dallmann and Herman 1978). The active substance in monarchs may be similar to, or identical with, either locust AKH or shrimp RPCH (Dallmann, Herman, Carlsen and Josefsson 1981), since both substances are very effective in mobilizing lipids in this species (see Fig 5). The effects of these two pure hormones in monarchs are most pronounced in diapause animals, where stored lipid levels are known to be high.

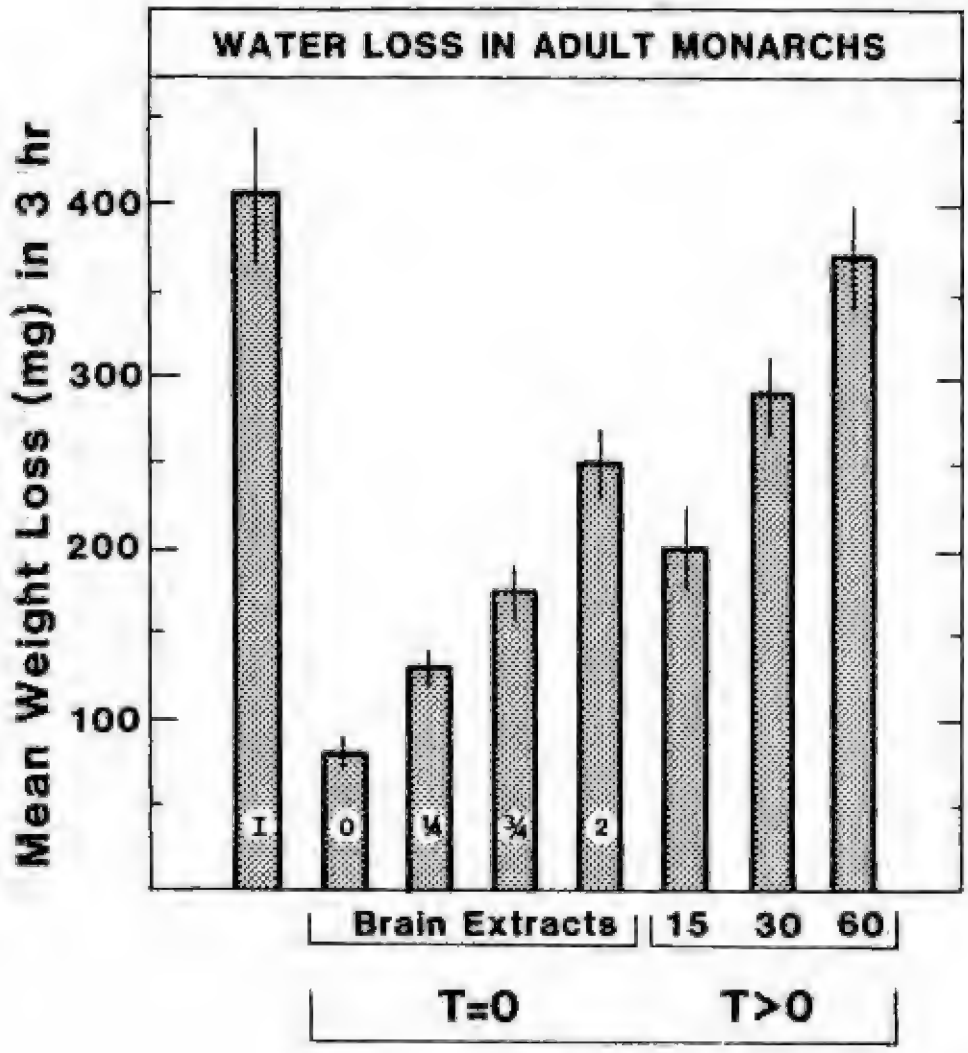

Figure 6

Some experiments indicating the existence of diuretic hormone in posteclosion monarchs. I = weight loss in intact control insects. In animals ligatured at the time of eclosion (T = 0) and injected with extracts containing 0 to 2 brain equivalents; a dose-response relationship is apparent. In animals ligatured to 15–60 minutes after eclosion (T > 0) progressively greater diuretic responses occur, indicating rapid posteclosion release of the active material. Mean n = 13.1; data from Dores et al. and Dores and Herman (1981).

Monarch Diuretic Hormone

A second neuropeptide appears to function as a diuretic hormone (DH) in adult monarchs. At eclosion the body weight rapidly diminished from over 1 gm to about 500 mg and our experiments have shown that this weight loss is principally due to water loss (Dores, Dallmann and Herman 1979; Dores and Herman 1981). Apparently a DH is released from the cephalic neuro-endocrine system within 15–30 min after eclosion, as illustrated in Figure 6. It is of interest that even though this DH activity can be extracted from heads of all stages of the adult cycle, it can only be shown to function as a DH at the time of eclosion, and not during the pronounced postfeeding diuresis which is characteristic of adults of this species.

Are the monarch AKH and the monarch DH the same molecule? Apparently not, since DH activity (unlike that of AKH) cannot be extracted in methanol and/or butanol, does not reside in molecules or gel filtration fractions with AKH activity, and is associated with fractions of apparently higher molecular weight (see Table 4).

Table 4
Comparison of Monarch AKH and Monarch DH

	AKH	DH
Stable After:		
Boiling	+	+
H_2O_2 treatment	+	+
Storage at 25°C	+	+
Inactivated by:		
Trypsin	+	+
Protease	+	+
Soluble in:		
Distilled H_2O	+	+
Methanol	+	−
Butanol	+	−
Mimicked by:		
Synthetic AKH	+	−
Synthetic RPCH	+	−
Monarch AKH fractions	+	−
Monarch DH fractions	−	+
Estimated Molecular Weight:	1000	3000

Data from Dallmann and Herman 1978; Dores, et al. 1979; Herman, unpublished.

Monarch DH appears to be a stable peptide with a molecular weight of about 3000 daltons; the apparent stability and relatively small size of this substance suggest that efforts to characterize the material may be rewarding.

Role of Hormones in Other Adult Lepidoptera

A limited number of other adult Lepidoptera have been examined to date, but the available data suggest that species other than monarchs also use a variety of hormones as regulatory agents. We have shown that the mourning cloak butterfly *(Nymphalis antiopa)* uses JH to regulate certain aspects of both male and female reproduction (Herman and Bennett 1975). We have also reported that the painted lady butterfly, *Vanessa cardui*, responds to JH, RPCH, locust AKH, and DH-containing extracts in a manner comparable to that found in monarchs (Herman and Dallmann 1981). In addition, Truman and coworkers have described in detail an eclosion hormone in adult Lepidoptera (Reynolds and Truman 1983), Nicolson (1980) has demonstrated the existence of DH in the cabbage white butterfly *Pieris brassicae*, Shapiro and Law (1983) have reported an effect of locust AKH in *Manduca sexta*, and several authors have presented evidence for JH regulation of some aspect of lepidopteran reproduction (Nijhout and Riddiford 1979; Engelmann 1983). Thus the

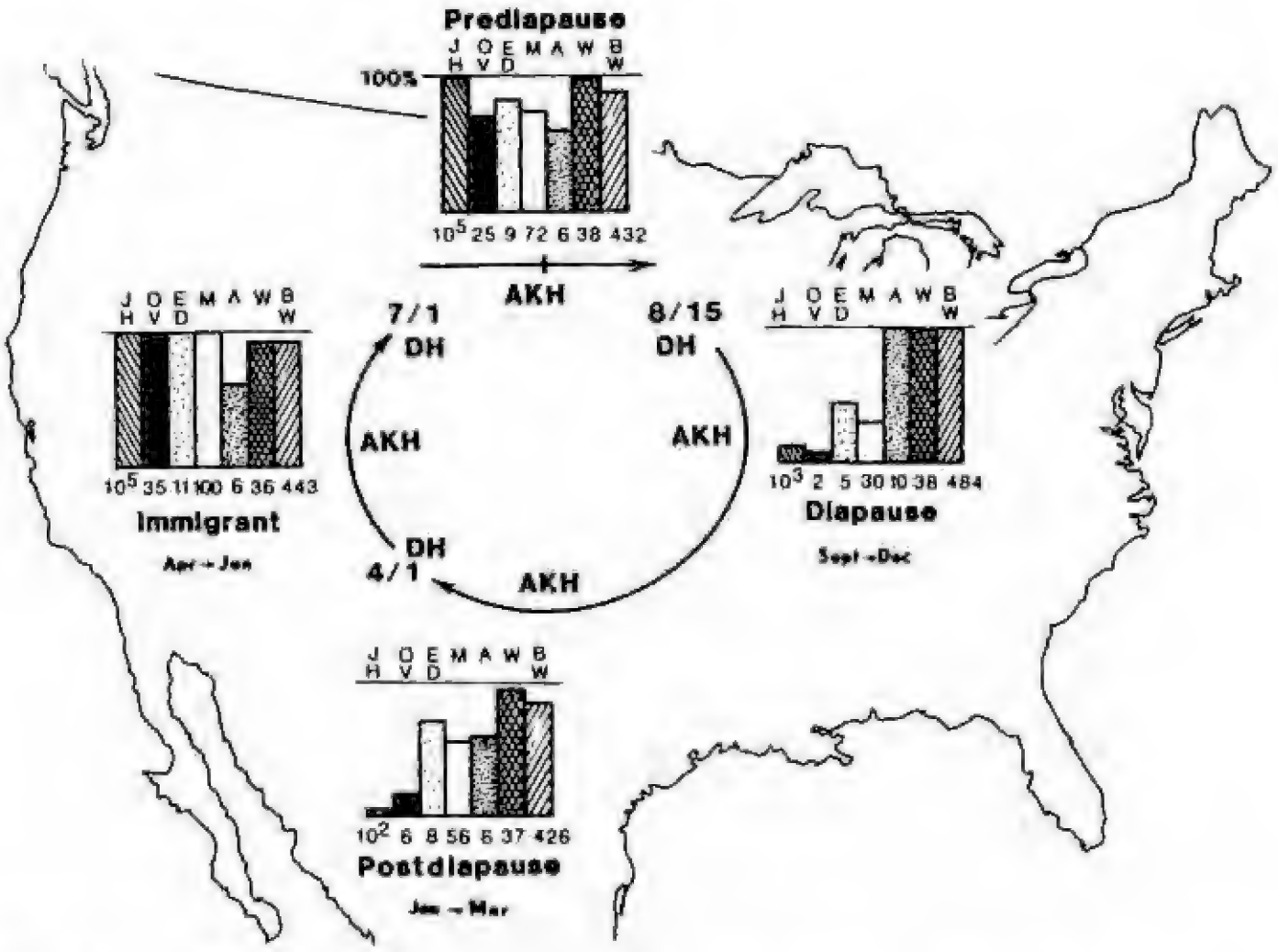

Figure 7

Summary of hormonally mediated events occurring during the annual adult cycle of the monarch butterfly. JH = juvenile hormone hemolymph titers in *Galleria* units; OV = ovarian wet weight in mg for both sexes; ED = ejaculatory duct wet weight in mg; M = percentage of mated females; A = longevity in weeks when held in summer conditions (only female data indicated); W = rear wing length in mm for both sexes; BW = whole body wet weight in mg for both sexes; DH = diuretic hormone activity; AKH = adipokinetic hormone activity. The graphs present approximate mean values, and indicate approximate percentage of maximal mean value observed during the year, for each of the four major stages in the life cycle.

available data from several laboratories indicate the existence of a variety of hormonal systems in at least several species of adults of this order.

DISCUSSION

Figure 7 summarizes our current understanding of the annual adult cycle of the monarch butterfly and of the hormonally mediated events known to occur in adults during this cycle. For convenience the figure implies that our data relate to both the eastern and the western monarch populations, but this relationship has yet to be documented. The cycle can be considered as beginning in Minnesota about July 1, when the first resident (prediapause) generation of the year typically emerges. From July 1 to August 15 this resident generation is characterized by high hemolymph JH titers, well-developed reproductive tracts in both sexes, a high level of mating, rapid aging, large wing size, and intermediate body weights. This generation is a highly

variable population in that all ages, including young, newly emerged, unmated individuals, and old monarchs nearing death, are present. It is the existence of these young and old animals in the population that results in less than maximal mean value for reproductive tract and body weights and for percentage of monarchs mated. The first generation requires the DH at emergence and it probably uses AKH (at least to some extent) to mobilize stored lipids. Both aging data and field studies indicate that at least one generation, and sometimes two (if the summer is long) form this resident prediapause population.

Most, if not all, of the adult monarchs emerging after August 15 in Minnesota are of the migratory diapause generation. These migratory animals have substantially reduced JH titers, a reduced level of reproductive tract development, and they are (prior to migration) infrequently mated. They possess large wings and high body weights, and our aging data indicate that at least the females have a reduced rate of senescence when placed in summer conditions. After feeding intensively for a few weeks, this population emigrates from Minnesota with small reproductive tracts, large amounts of stored lipid, large wings, and high body weights; they are presumably admirably equipped for long migratory flights. In addition, the existence of the diapause condition in these monarchs prevents an inappropriate response to short-term suitable environments and thus reduces the likelihood of futile reproductive activity, with its associated depletion of stored reserves, in monarchs bound for the overwintering colonies. This generation also requires the DH at emergence, and these animals use the AKH to mobilize stored lipid reserves during migratory flight.

Adult monarchs reach the overwintering sites in diapause, typically in October or November. At this time, mating levels increase from the low levels of September to about 50%, giving a mean value for the entire diapause period of about 30%. The reason for this early enhancement of mating activity in the newly formed colony is not clear, but it may provide a mechanism of nutrient transfer (Boggs and Gilbert 1981) designed to enhance female survival during the overwintering period.

After colony formation, diapause is broken in December (males) or January (females), and both sexes enter the postdiapause period. At this time the monarchs are poised to respond to suitable environments, but such environments do not normally occur until late February or early March. In the postdiapause period female hemolymph JH titers and reproductive tract development remain low, and female longevity in summer conditions is comparable to that of prediapause animals. Male and female body weights decline noticeably as reserves are utilized. Unlike females, postdiapause males produce large amounts of JH during at least part (February) of the postdiapause period, and this event is reflected in the high rate of male reproductive gland growth, the enhanced level of mating, and declining male longevity. It would appear that the reduced sensitivity of females to JH and the low level of production of JH in postdiapause females may be adaptations which allow the majority of the females of leave the overwintering site in a condition comparable to that of a newly emerged summer prediapause resident in Minnesota. By contrast the postdiapause male apparently expends his energy and may shorten his life in an effort to ensure successful mating and, perhaps, also to enhance survivability of the female.

Colony dispersal by postdiapause adults is presumably followed by a high level of oviposition in the southern portions of the breeding range, since clear indications of reproductive tract development are seen in both males and females at or near the time of leaving the colonies. Assuming developmental rates of egg, larvae, and pupae comparable to those observed in the north, and colony dispersal around the first of March, it seems reasonable to estimate that the first new generation of the annual cycle probably emerges in early April in the southern portion of the breeding range. This generation apparently migrates north and provides most of the immigrants arriving in Minnesota in late May or early June. Unlike southward migrants of the previous fall, this immigrant generation has high levels of hemolymph JH, very well-developed reproductive tracts, no virgins, and smaller wings than other stages of the cycle. As indicated by mean body weights, most of these animals are relatively young, too young to have been reproductively active from about the first of March until late May or early June (i.e., 10−14 weeks). This immigrant generation, like all others, requires DH at emergence and presumably uses AKH to mobilize reserves during the northward migration.

ACKNOWLEDGMENTS

The above review is based upon the efforts and ideas of several scientists who have worked with me on monarchs over the past decade. These individuals are Drs. John F. Barker, Robert M. Dores, C. Genevieve, D. Johnson, Louise Rollins-Smith, and Charles A. Lessman, and also Steven W. Dallmann and Philly Peng in the U.S.A., and Drs. Jens Carlsen, Mogens Christiansen and Lars Josefsson in Denmark. Ransom L. Gilbert, Emily Sherwood, Robert F. Ardery and Ella E. Conyes also made significant contributions to this research. Finally, the assistance of Mr. Paul Cherubini, who provided us with California monarchs for several years, has been essential to our work and is highly appreciated.

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ENDOCRINE INFLUENCE ON FLIGHT BEHAVIOR

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ABSTRACT

Migratory behavior and/or flight muscle metabolism have been shown to be influenced by a number of neuroendocrine factors. Juvenile hormone stimulates migratory behavior in ***Oncopeltus fasciatus***, ***Hippodamia convergens***, ***Eurygaster integriceps***, and ***Danaus plexippus***. However, the same hormone has no effect or stimulates flight muscle degeneration in other species. In those species in which JH has been shown to have an effect on flight behavior, it is also necessary for oogenesis. It may serve to coordinate oogenesis, adult diapause and migration, particularly in colonizing species. Other neuroendocrine products that have been implicated in control of flight behavior or flight metabolism are (1) ecdysone, (2) adipokinetic hormones produced in the corpora cardiaca, and (3) octopamine. Octopamine may well prove to be a primary link between the endocrine system and the flight motor itself since injections of this biogenic amine directly into the metathoracic ganglion of locusts induces rhythmic stepping behavior or flight behavior (Sombati and Hoyle 1985).

INTRODUCTION

Migratory flight behavior in insects has been characterized as persistent, straightened-out movement accompanied by and dependent upon an inhibition of response to "vegetative" stimuli that will eventually arrest movement (Kennedy 1961). This definition, which was the result of Kennedy's elegant and painstaking analysis of aphid flight behavior, has been revised (expanded) by Kennedy in the first chapter of this book. The original definition has been used, however, in a number of laboratory analyses of migratory behavior to distinguish migratory from trivial flight. The criteria that Kennedy put forward, i.e., the long duration and the undistractedness of migratory flight, have been used in a number of systems to identify migrants (see Rankin and Singer 1984 for review). In insects in which routine or trivial movement is accomplished by walking, hopping, or short bursts of flight rather than by sustained continuous flight, ***duration*** of tethered flight has proved to be a good indicator of migratory tendency (Dingle 1965, Rose 1972, Rankin and Rankin 1980, Davis 1980). Results of flight tests of known ***H. convergens*** migrants from the field (Rankin and Rankin 1980a and b), the observation that milkweed beetles actually caught in flight make longer tethered flights than beetles randomly collected on the substrate (Davis

1980), and data outlined by McAnelly (this volume) and McAnelly and Rankin (in press) for *M. sanguinipes*, strongly support the assumption that long-duration tethered laboratory flights are performed by insects that would migrate in the field and vice versa. Analysis of flight behavior on the basis of duration of tethered flight has been most useful where flight tendency of individuals in a population fall into two reasonably distinct categories: long-duration sustained flight and brief flights of several minutes or less, the former representing migratory behavior, the latter, trivial flight. For example, *Oncopeltus fasciatus* that will not make a migratory flight typically refuse to re-open their wings after 2 min or less of tethered flight; a few continue to fly for 5−10 min. However, if an insect flies for 30 min, it will almost always continue much longer. A flight duration longer than that of trivial flights but considerably less than flight to exhaustion can thus be established as a criterion for migratory behavior.

Juvenile hormone (JH), the secretory product of the corpora allata (CA), has been shown to induce such long-duration tethered flight behavior in three species of insect migrants, *Oncopeltus fasciatus* (Caldwell and Rankin 1972), *Hippodamia convergens* (Rankin and Rankin 1980) and *Danaus plexippus* (Rankin, McAnelly and Bodenhamer in press). Polivanova and Triseleva (1984) have shown a role for JH in the control of migratory behavior of the wheat pest, *Eurygaster integriceps* as well. Some authors (Cassier 1963, 1964; Odhiambo 1966; Wajc and Pener 1971) have also implicated the corpora allata, and therefore JH, in locust flight behavior and/or locomotor activity, but the flight test protocol is somewhat ambiguous and for other reasons this work is controversial.

In addition to JH, a number of other hormones have been implicated in the control of flight behavior or metabolism, including secretory products of the corpora cardiaca, the biogenic amine, octopamine, and ecdysteroids. Although the particular distinction between migratory and trivial flight behavior has not always been made directly in experiments involving these other neuroendocrine products, an effect specifically on migratory behavior can often be inferred.

This paper will review endocrine involvement in presumed migratory flight in insects with some attention given to the hormonal control of flight metabolism as well. (See Herman, this volume, for a discussion of this issue in the monarch butterfly.)

JUVENILE HORMONE EFFECTS ON MIGRATORY BEHAVIOR

Juvenile hormone may have different effects on flight behavior or the flight apparatus itself in different species. For example, juvenile hormone has been implicated in the control of wing development in wing-polymorphic insects.

Southwood (1961) suggested that brachypterous European gerrids are either juvenilized adults (metathetely) or neotenous, a larval form with adult characters (prothetely). Wing muscles are absent in brachypters; some though not all macropters are migrants. The flight muscles of macropters are resorbed as the ovaries mature. Wing buds of both morphs appear identical in 5th instars but there seems to be no growth of wing tissue between the penultimate and imaginal molts in brachypters

(Brinkhurst 1963). Southwood suggested that brachyptery is due to either an excess of JH, if metathetely, or a reduced effect of this hormone, allowing premature metamorphosis, if prothetely. Since brachyptery is often associated with colder climates and higher altitudes, he concluded that low temperatures prolong the larval state and thus exposure to JH. He therefore proposed that brachypters are metathetelous adults. Indeed, short-winged adults can be produced in ***Rhodnius*** by JH application to 5th instar nymphs, but treatment effects are not confined to wing morphology; suppression of other adult characters in the cuticle, genitalia and sense organs also occurs (Wigglesworth 1961). In spite of the abundant speculation about the physiological basis of wing polymorphism in gerrids, very little actual experimental work has been done to address this question.

Lees (1967) suggested that activity of the maternal corpus allatum (CA) influences production of alate and apterous aphids. Since apterous aphids appear to retain many larval characters (e.g. underdeveloped wings), high maternal hemolymph titers of JH were thought to stimulate aptery in the offspring. However, since Lees originally put forth this idea, a large body of somewhat conflicting data has accumulated and Lees himself showed (Lees 1980) that high concentrations of JH or JH mimics applied to ***M. viciae*** were ineffective in causing alate producers to switch to exclusive production of apterae. He concluded that JH is not involved in the switch mechanism. Hardie (1980, 1981b) similarly concludes that JH is not involved in the alate/apterous polymorphism in virginoparous generations of ***A. fabae***. Mackauer, Nair and Unnithan (1979) reported that applications of the anti-allatotropin, precocene II, to virginoparous ***Acyrthosiphon pisum*** caused a switch in production from apterae to alatae and this could be partially reversed by high doses of JH I. Precocene did not, however, have other antiallatotropic effects. The conclusion by Mackauer et al. (1979) that JH is involved in wing development of virginoparae directly conflicts with that of Lees (1980) and Hardie (1981b) though all three studies were done with different species.

Control of wing development may also be post-natal in aphids. Several studies have involved hormone treatment of early instar nymphs, conducted to gain an understanding of the mechanisms of apterous development, as well as the observed post-natal induction of alates. Lees (1980) found that treatment of any instar of ***Megoura viciae*** before the early 4th with JH or JH mimic induces wing deformities and/or supernumery molts. Production of malformed wings is not, however, equivalent to induction of neoteny (Lees 1980). As in the Heteroptera (see below), Lees found many other aphid characters to be affected by exogenous JH treatment of nymphs, particularly the genitalia. He again concluded that JH is probably not the key to post-natal induction of aptery (Lees 1980). Post-natal JH treatment to *A. **fabae*** presumptive gynoparae, however, did induce aptery without juvenilization if administered before the 2nd day of the 2nd instar (Hardie 1980). Thus, exogenously applied JH may affect adult morphology and reproductive form in aphids but whether or not JH is a major determining factor of wing development under natural circumstances is not clear, nor is the timing of its putative action, whether pre- or post-natal. Indeed, there may be substantial species differences in the role of JH and/or the timing of its action in the

control of aphid alary polymorphism.

In several insects, JH has been shown to affect flight muscle development or histolysis in the adult stage. In ***Ips confusus*** (Borden and Slater 1968) and ***Dysdercus fulvoniger*** (Davis 1975), for example, high juvenile hormone levels, presumably associated with the onset of oogenesis, induce flight muscle degeneration. In contrast, in the Colorado potato beetle, ***Leptinotarsa decemlineata*** (de Wilde and de Boer 1961, 1969; de Wilde, Staal, de Kort, DeLoof and Baard 1968), juvenile hormone seems to be necessary for flight muscle regeneration after diapause. It may also be involved in migratory behavior, but that question has not been specifically addressed for ***Ips***, ***Dysdercus***, or ***Leptinotarsa***.. In the cockchafer, ***Melolontha melolontha*** the state of activity of the corpus allatum (CA) affects the orientation of flight (Stengel 1974) either towards or away from oviposition and feeding sites.

The apparent relationship of diapause and migration, and Johnson's (1966) suggestion that migration was prereproductive because migratory behavior was induced by a lack of JH, led to an investigation of the effect of JH on flight behavior in a typical insect migrant, ***Oncopeltus fasciatus*** (Caldwell and Rankin 1972). These studies have since been extended in my laboratory to two other migrants, ***H. convergens*** (Rankin and Rankin 1980), and ***Danaus plexippus*** (Rankin, et al. in press), and in Russia, Polivanova and Triseleva (1984) have done similar studies on ***Eurygaster integriceps***.

Oncopeltus fasciatus

The summer range of ***Oncopeltus fasciatus*** extends from Canada to Central America but it does not survive winter conditions in temperate areas. Dingle (1966, 1968) has shown, on the basis of laboratory flight tests and some highly suggestive field evidence, that a portion of the resident southern population migrates north in the spring and colonizes the very abundant milkweed fields in the north. It appears in Iowa milkweed patches in late June or early July and the population rapidly expands, reaching a peak in early September. By October, ***O. fasciatus*** has nearly disappeared from this area, apparently due to southward flights of much of the population.

Long-duration tethered flight behavior has been used as a criterion for migratory behavior in this species (Dingle, 1965, et seq.; Rankin 1974, et seq.; Palmer, this volume; Slansky 1980), this type of flight behavior being largely restricted to the post-teneral, prereproductive period. In response to short photoperiods, ***Oncopeltus*** undergoes an adult reproductive diapause that provides a considerably longer period of time prior to egg maturation during which females will make long flights and also increases the percentage of individuals of both sexes in laboratory populations that make a long flight at some time during that period (Caldwell and Rankin 1972). The combination of short photoperiod and low temperatures in the fall probably induces migratory behavior in most of the northern population. Although ***Oncopeltus*** displays a classical oogenesis flight syndrome, performance of long-duration flight does not elicit a reduction in total reproductive output or longevity, nor does it induce a delay in first reproduction (Slansky 1980). Furthermore, Palmer (this volume) has shown

that selection for long wings results not only in increased frequency of long-duration flight in the population but also in a correlated increase in reproductive output.

Food quality or availability can also greatly affect flight and reproduction. When fed on sub-optimal food, green pods or flowers, female *Oncopeltus* delay reproduction and will make long flights even in long-day and relatively high-temperature conditions that would normally induce reproduction. Since the first northern colonizers typically arrive in Iowa in late June or early July when temperatures are high and photoperiods are approaching the longest of the year, it is likely that food quality (flowers and green pods at this time) is an important factor in stimulating northward flights in the spring. By this same mechanism, flight can also be stimulated among reproductively mature residents by a food shortage, thus greatly increasing the probability of finding new food sources.

Experiments involving gland extirpations and implantations showed that juvenile hormone (JH) has a dual role in adult development of this species. The hormone stimulates migratory behavior in both sexes and ovarian development in the female (Caldwell and Rankin 1972; Rankin 1974 et seq.; see Fig 1).

As the ovaries attain their full development in the female, further migratory flight is inhibited, although short appetitive flights still occur. JH titer determinations on pooled hemolymph samples from adult *Oncopeltus* exposed to different photoperiod regimens indicated that long photoperiods result in immediate increase in hemolymph titers of the hormone (associated with rapid onset of oviposition behavior), while short photoperiods bring on a more gradual increase in JH levels following adult emergence. Short photoperiods enhance migratory flight and delay onset of reproduction (Rankin and Riddiford 1978). In any photoperiod regime, migratory flight typically occurs during periods of intermediate hormone titers. It would appear that lower titers of JH or shorter exposure times are necessary to stimulate flight before reproductive development, which ultimately inhibits long flights. Selection for 4 generations for late onset of migratory flight behavior resulted in a correlated delay in onset of reproduction and a delay in the associated rise in JH titers (Rankin 1978). When *Oncopeltus* are starved, JH titers decline and oogenesis ceases (Rankin and Riddiford 1977). Flight activity first increases and then decreases to very low levels. JH replacement therapy to starved animals stimulates migratory flight behavior and oogenesis.

Treatment with the chemical allatectomizing agents Precocene I and II (Bowers 1976; Bowers, Ohta, Cleere and Marsella 1976) not only caused cessation of oviposition and resorption of oocytes but also produced a decrease in long-duration flight behavior in the population. Flight could be restored to high levels by JH replacement therapy (Rankin 1980; Fig 2). Like starvation, precocene treatment stimulates a transient increase in frequency of migratory behavior and in the duration of shorter flights. This increased flight behavior after precocene treatment can be quite prolonged under some circumstances and seems to be associated with an incomplete inhibition of JH production (as determined by CA size and state of ovarian development, Rankin, unpublished results). The precocene experiments indicate that JH is necessary for both long-duration flight behavior and reproduction in *Oncopeltus fasciatus*.

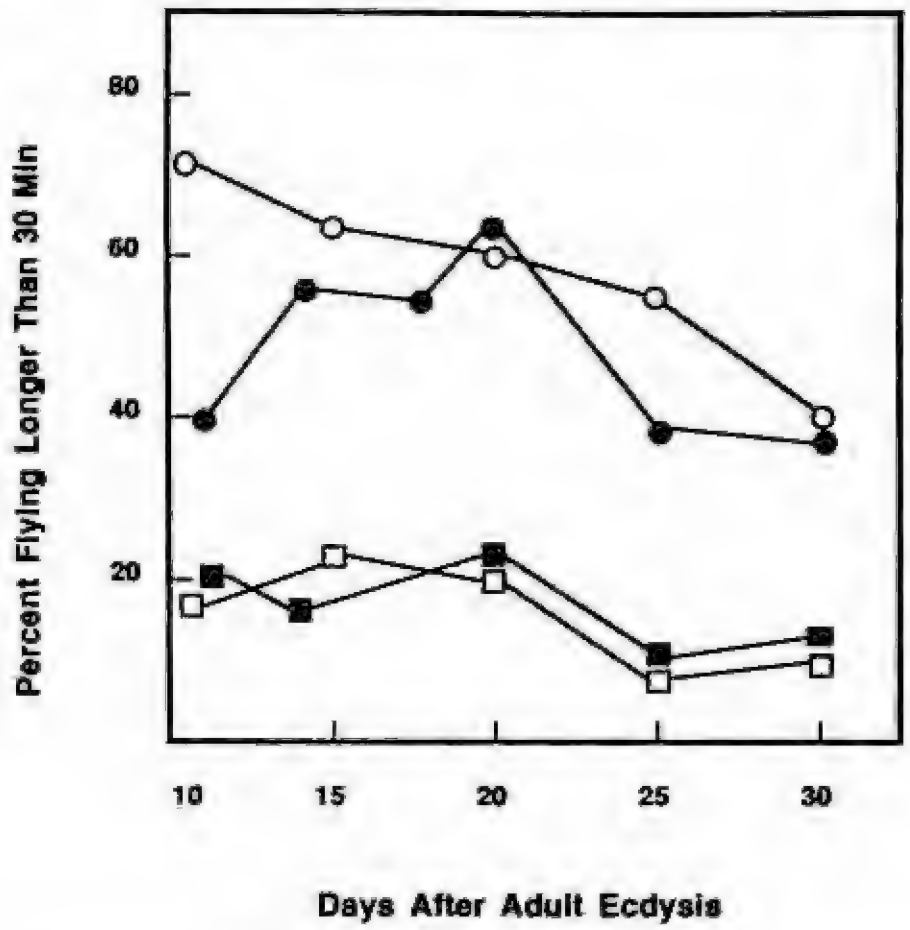

Figure 1

The effect of juvenile hormone mimic applications on flight behavior of intact male and female and ovariectomized female *Oncopeltus fasciatus* (open symbols = ovariectomized females; solid symbols = males; circles = JHM treated; squares = acetone-treated controls). Animals were reared under 12:12 L:D photoperiod, at 22°C. Ovariectomies were performed on fifth instar nymphs. (Redrawn from Rankin 1974).

Hippodamia convergens

Another insect in which the role of JH in migratory flight has been examined is the ladybeetle, ***Hippodamia convergens*** (Rankin and Rankin 1980). This insect is one of the most widespread of the American coccinellids, occurring throughout the western, central and southern United States. It is an economically important predator of aphid and mite pests on cultivated crops and in fact is commercially available as a natural control agent for such pests.

Adults emerge from "hibernation" sites in the spring and migrate up to hundreds of kilometers to areas of aphid infestation (Hagen 1962) where they may develop high densities (Dickson, Laird and Pesho 1955). As aphid populations decrease, the coccinellids move to neighboring habitats. Such movements may occur several times in a season and, depending on food abundance, the species may be uni- or multivoltine. If prey are unavailable or scarce, young adults enter reproductive diapause and an extended migratory phase during which they move to mountaintop aggregation sites. Diapausing beetles may remain at the hibernation sites from 6 to 9 months until they migrate back to lower altitudes (Hagen 1962, Rankin and Rankin 1980b). Some type of diapause development seems to be involved in the return of the migratory response at this time (Rankin and Rankin 1980a, b).

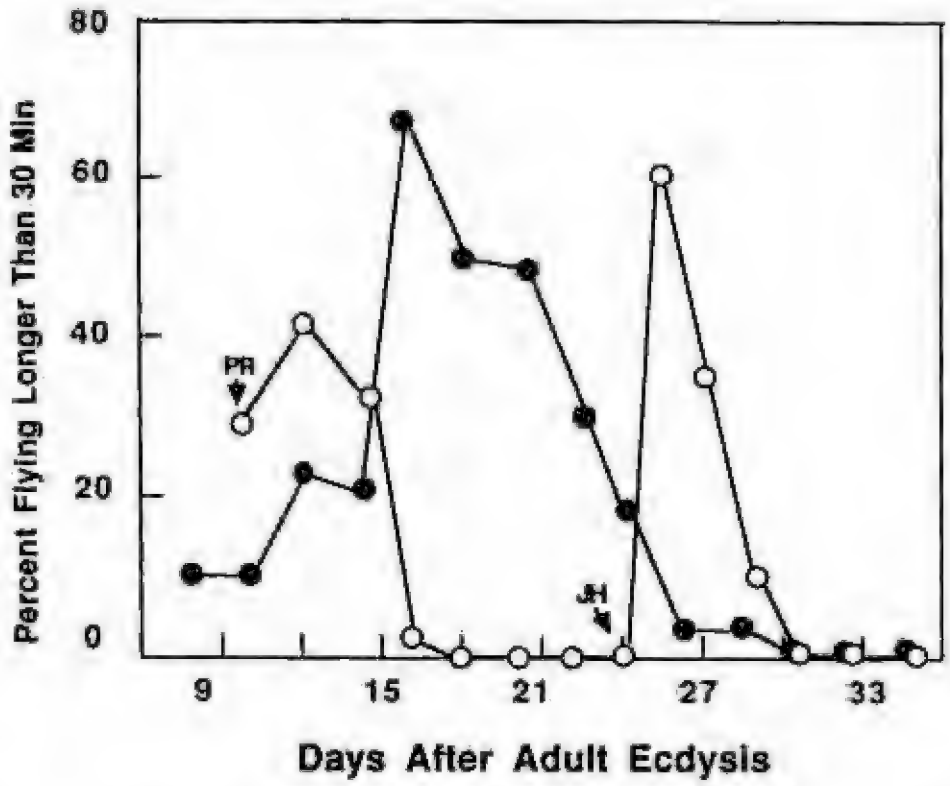

Figure 2

The effect of precocene I and II and juvenile hormone replacement therapy on flight behavior of *Oncopeltus fasciatus* (open circles = precocene and JHM-treated animals; solid circles = acetone-treated controls).

Laboratory tethered-flight tests can be used as an assay for migratory behavior. Beetles that fly 30 minutes on a tether will nearly always fly much longer. It appears that migration to the aestivo-hibernation sites is accomplished primarily by newly emerged (prereproductive female) beetles. As is true for many insect migrants, long duration tethered flights tend to occur most frequently among prereproductive *H. convergens* females. Long day length and high quality food result in a sharp decline in flight after 1 week, by which time oviposition has begun. Under short photoperiod and/or poor food quality (frozen aphids) long flights continue for some time in the population. Photoperiod seems only to influence the duration of the long-flight phase when food quality is optimal. When this is the case, short photoperiod greatly lengthens the period of time in which beetles will make long flights, although the percentage of long fliers in the population is lower when food is optimal than when it is not. When food quality is poor, flight activity is enhanced under either photoperiod regime to quite high levels. Thus the beetles do respond to photoperiod under some conditions, but food quality seems to be the primary cue which triggers migratory behavior. Similarly, ovarian development is dependent upon food quality, photoperiod having little, if any, effect; *H. convergens* can be reproductive under both long and short-day conditions (Rankin and Rankin 1980b).

Under long days there seems to be a clear oogenesis-flight syndrome in this species, i.e., ovarian development is inversely correlated with flight activity (Fig 3a). Under short photoperiods, peak flight activity occurs in females with partially developed, rather than completely undeveloped ovaries. Furthermore, some flight activity continues in the short-day population until ovarian development is complete (3.0 mg; Fig 3a), while it virtually ceases in the long-day animals by the time the reproductive tract has attained 1.5−2.0 mg fixed wet weight. Thus the oogenesis-

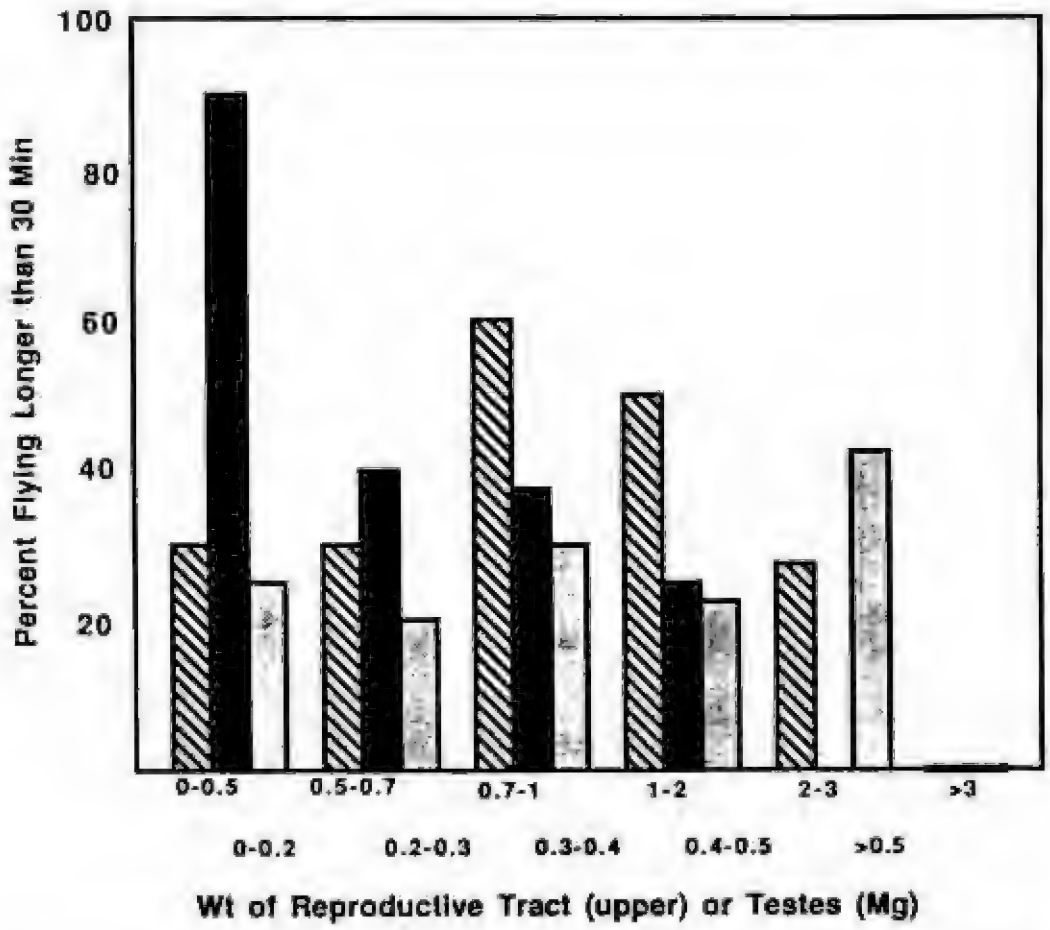

Figure 3

Relationship of reproductive tract development to long-duration tethered flight behavior in ***Hippodamia convergens***. Flight activity of females collected in March (short-day photoperiod; dark shaded bars; n = 38) and in mid-summer (long-day photoperiod; striped bars; n = 50) around Austin, Texas, with respect to weight of the fixed reproductive tract. Flight activity of males collected in mid-summer (light, shaded bars) (long-day photoperiod; n = 35), with respect to testes weight. (From Rankin and Rankin 1980b)

flight syndrome is less pronounced and flight continues longer in the population under short photoperiods (Rankin and Rankin 1980b).

Juvenile hormone is necessary for ovarian development in this species (Fig 4) although, as with many beetles, a brain factor is also necessary for completion of oogenesis (S.M. Rankin 1982). Topical application of a JH mimic (JHM) to *H. convergens* stimulated ovarian development in females and a significant increase in long-duration flight behavior in both sexes (Fig 5). Topical application of precocene II to *H. convergens* inhibited flight activity and oogenesis for about 10 days; JHM (altosid) treatment to precocene treated beetles significantly increased their migratory behavior over that of precocene-treated or acetone-treated controls and also stimulated oogenesis (Fig 6). These results indicate that JH stimulates migratory flight behavior in this species along with reproductive development. It is likely that the hormone serves to coordinate migration with reproduction in the young adult. Higher doses of JHM (10 μg/animal) seemed to have a dual effect in females, increasing flight, but stimulating ovarian development so rapidly that long-duration flight behavior is inhibited within a few days. The sharp decline in flight on day 8 among females given 10 μg JHM may have been due to such an ovarian-based inhibitory effect (Fig 5; Rankin and Rankin 1980a).

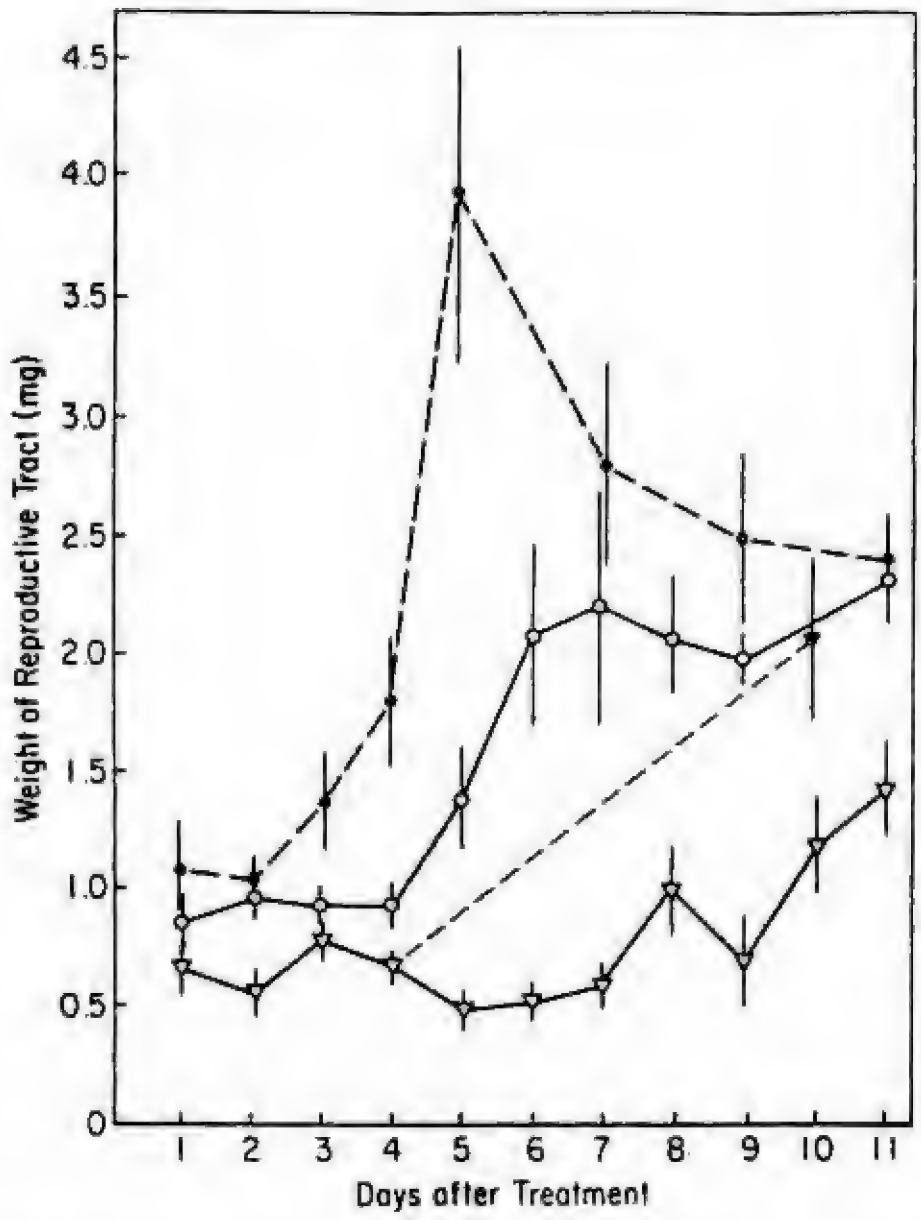

Figure 4

Effects of 10 μg applications of precocene II and JHM on weight of the entire fixed reproductive tract of female *H. convergens*. Closed circles indicate JHM-treated animals; open circles, acetone-treated controls; open triangles, precocene-treated animals; the solid triangle connected to the precocene treatment group indicates precocene-treated animals given JHM repacement therapy on day 4. Bars, SEM. (From Rankin and Rankin 1980a).

In one group of females collected shortly after their arrival at the hibernacula and treated immediately and repeatedly with JHM, the flight response to JH treatment was sustained and did not involve cessation of flight after several days (Fig 5c), nor was there substantial ovarian development (Table 1; Rankin and Rankin 1980a). In contrast, all other animals used had been stored at low temperatures in diapause for several months prior to testing, and the two groups were significantly different in their flight activities ($p < 0.001$, Mann-Whitney U). We have found that among animals collected from aggregation sites in Texas, flight activity is very low when beetles are newly arrived at the aggregation sites. There seems to be a gradual increase of the migratory response during diapause. The increase in responsiveness to migratory stimuli may be due to a gradual rise in JH titers or a change in sensitivity to the hormone similar to that observed in diapausing monarch butterflies (Herman 1981). The relatively moderate increase in ovarian weight among newly aggregated females in response to high and repeated applications of JHM (Table 1) tends to support this suggestion.

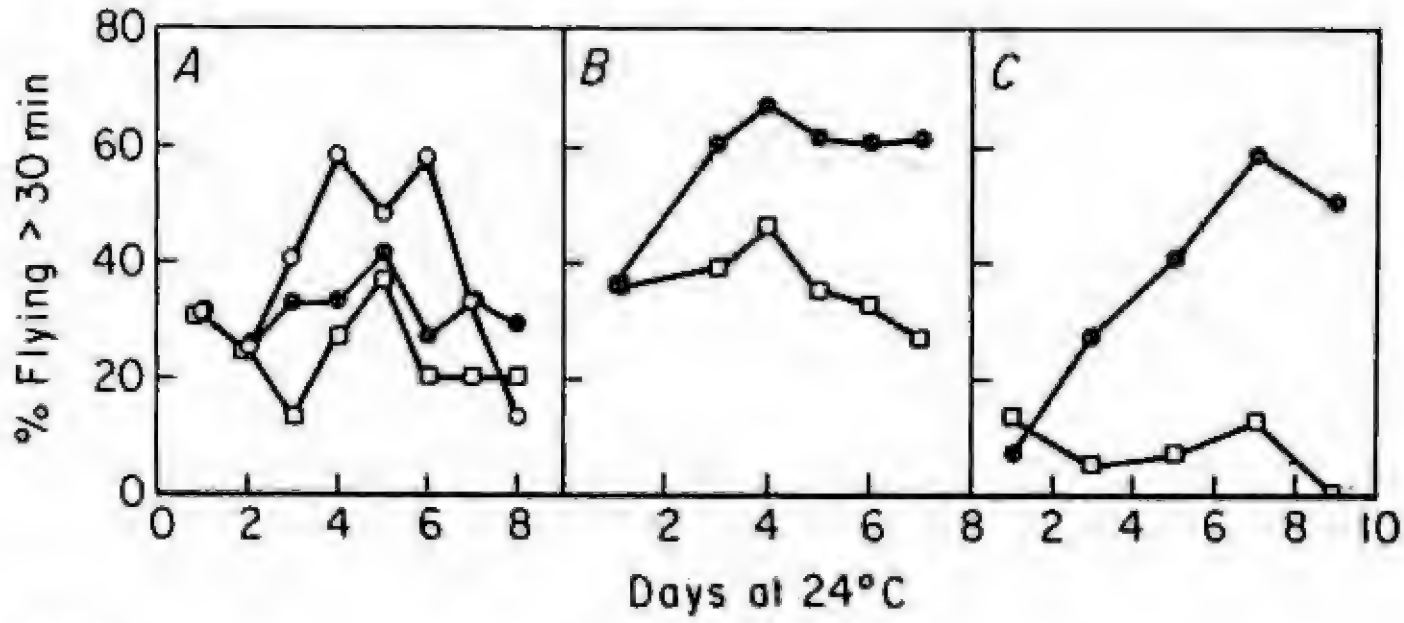

Figure 5

Effect of JHM on flight behavior of *H. convergens*.

a. females (open squares, solid line = acetone-treated, n = 15; triangles, broken line = 5 µg JHM day 2, n = 15; diamonds, solid line = 10 µg JHM day 2, n = 15)

b. males (open squares = acetone-treated, n = 30; solid triangles = 10 µg JHM on day 2, n = 30).

c. females collected in June from the hibernacula, given repeated applications of JHM (open squares = acetone treated days 2,4,6, and 8, n = 30; solid triangles = 10 µg JHM on days 2,4,6 and 8, n = 30). (From Rankin and Rankin 1980a)

The increased flight behavior of JHM-treated males occurred without a subsequent depression in flight activity (Fig 5b), suggesting that in the absence of ovaries, flight stimulation by JH may be more prolonged (Rankin and Rankin 1980a). This is similar to the effect of JH in male and ovariectomized female ***Oncopeltus fasciatus*** (Rankin 1974). As with ***O. fasciatus***, precocene treatment inhibited both oogenesis and flight behavior in ***H. convergens***, and JH replacement therapy restored both (Fig 6). Like ***Oncopeltus fasciatus***, there is clearly a coordinated stimulation of both long flight behavior and reproductive development in this species. This, in combination with the "relaxation" of the oogenesis flight syndrome in short photoperiods suggests that selection has acted to maximize both flight and reproduction in the migrant colonizer and has done so through the neuroendocrine system.

ECDYSONE

Another hormone that has been implicated in the control of migratory behavior in locusts is ecdysone. Implanting active prothoracic glands seems to depress locomotor activity, both marching in nymphs (Carlisle and Ellis 1963) and tethered flight in adults (Michel 1972), suggesting that ecdysone may inhibit migratory behavior. However, in the latter experiments the differences were not striking and no sham implants of other tissues were done. Since such a decrease in activity could be caused by many factors including injury, these results are somewhat inconclusive. Evidence of a direct effect of ecdysone on the nervous system was reported by Haskell and Moorehouse (1963), however, who found that hemolymph with presumed high ecdysone activity caused a marked increase in ventral ganglion interneuron firing and a

Table 1
Effects of JHM treatment on the mean weight of the reproductive tract in *H. convergens* (from Rankin and Rankin 1980).

Treatment	Weight of tract mg ± SD
Tested in March	
Treated on day 2 only	
10 μg JHM/female	2.40 ± 0.18
1 acetone/female	0.82 ± 0.09
Tested in July	
Treated on days 2,4,6 & 8	
10 μg JHM/female	1.25 ± 0.24
1 acetone/female	0.65 ± 0.01

marked decrease in motor output to the extensor tibialis muscle of the locust metathoracic leg. This would have had the overall effect in the intact animal of decreasing locomotor activity—a very commonly observed correlate of onset of ecdysis in arthropods generally. Since ecdysone has been shown to be present in the adult form of many insect species and associated in one or more ways with reproduction (See Downer and Laufer 1985 for extensive reviews), it is not inconceivable that ecdysone could be involved in the inhibition of flight by the mature ovaries. Such an effect of ecdysteroids in adult insects has never been demonstrated, however. Indeed, in ***Oncopeltus fasciatus***, injections of from 0.01 μg to 5 μg ecdysone or up to 20 μg 20-hydroxyecdysone had no effect on flight behavior of either sex (Rankin, unpublished results). This possibility should, however, be re-examined in acridids.

ADIPOKINETIC HORMONES

Besides juvenile hormone and ecdysone, two other neuroendocrine factors have been reported to directly or indirectly influence flight behavior in insects: (1) the adipokinetic hormone first described in locusts and (2) most recently, the indole amine octopamine. The Effect of the Locust Adipokinetic Hormone is probably not directly on flight behavior per se but rather on flight metabolism, although the presence of the corpora cardiaca (CC) is said to be necessary for long-duration flight in locusts (Goldsworthy, Johnson and Mordue 1972). AKH controls lipid mobilization from the fat body, formation of the primary lipid transport protein in the hemolymph and probably uptake and utilization of lipid by the flight muscle. It is produced in the corpus cardiacum (CC) and its release is under control of the NCCI and II, probably via octopaminergic synapses (Goldsworthy 1985). Removal of the CC decreases flight

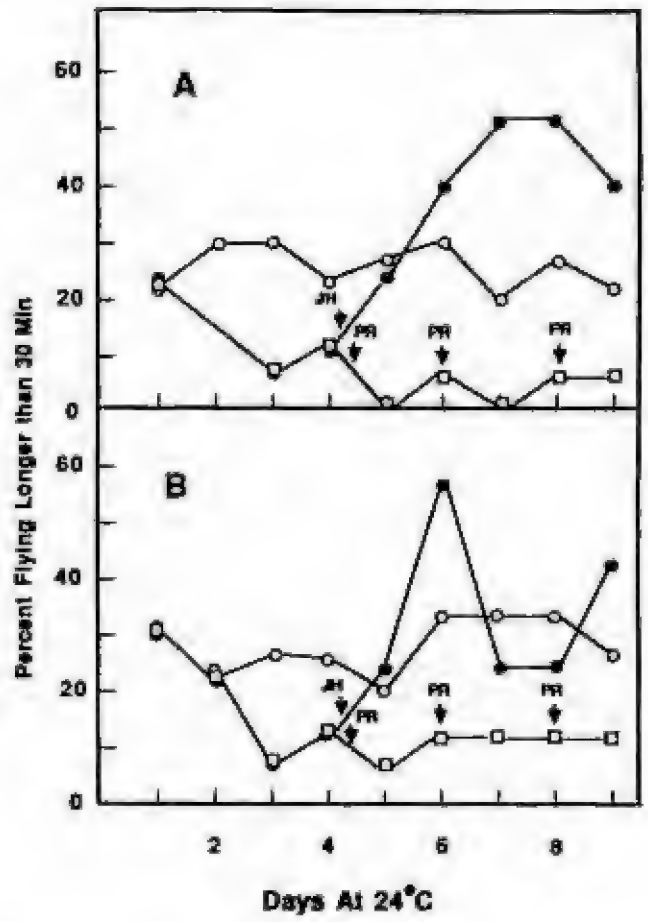

Figure 6

Effects of 10 μg applications of precocene II administered every 2 days or of precocene II followed by JHM treatment, on flight behavior of *H. convergens* males (a) or females (b) (redrawn from Rankin and Rankin 1980).

performance (speed on a round-about) of locusts (Goldsworthy et al. 1972).

In locusts the primary fuel for long-duration flight is lipid, specifically diacylglycerols. Carbohydrate is metabolized in short flights and the initial stages of long flight, but long, presumed migratory flight involves a switch to lipid fuel (Mayer and Candy 1969a; Jutsum and Goldsworthy 1976; Houben 1976; Van der Horst, Baljet, Beenakkers and Van Handel 1978; Van der Horst, Van Doorn and Beenakkers 1978) that appears to be controlled by AKH (Mayer and Candy 1969b, Beenakkers 1969) and possibly octopamine (Orchard and Loughton 1981).

Goldsworthy (1985) points out that to compensate for the rather long diffusion distances and low pressure inherent in the insect open circulatory system, a steep concentration gradient of flight fuel between the hemolymph and flight muscles is necessary. High hemolymph concentrations of diacylglycerols, which are virtually insoluble in aqueous solutions, is achieved by the formation of lipoprotein complexes in the hemolymph. AKH is involved in release of diacylglycerols from the hemolymph, formation of a specific lipid transport protein, and possibly in promoting lipid metabolism in the flight muscle.

AKH is released shortly after flight begins; a flight of only 2 min is sufficient to elevate hemolymph levels of the hormone and diacylglycerol (Jutsum and Goldsworthy 1977). The NCCII carries axons that synapse in the glandular lobe of the CC and have cell bodies in the protocerebrum (Rademakers 1977 a, b). Although only the NCCII has been shown to stimulate AKH release in vitro, both the NCCI and II must be cut in order to prevent release (Goldsworthy, Johnson and Mordue 1972).

AKH is a blocked decapeptide, one of a family of structurally related compounds that have been isolated from the CC of other insects and from some crustaceans. AKH activity has been reported in the beetle ***Tenebrio molitor*** (Goldsworthy, Mordue and Guthkelch 1972), the monarch butterfly ***Danaus plexippus*** (Dallmann and Herman 1978, see also Herman, this volume) and the tobacco hornworm moth ***Manduca sexta*** (Beenakkers, Van der Horst and Van Marrewijk 1978). Extracts of ***Periplaneta*** CC cause AKH effects in locusts but they decrease hemolymph lipid in the roach itself (as does locust AKH) (Downer 1972, Downer and Steele 1975). ***Carausius morosus*** CC extracts have no effect on lipid or carbohydrate levels in that insect but have AKH effects in locusts and a hypolipemic effect in roaches (Gäde 1979). Thus a small family of similar peptides seem to elicit a variety of effects in different insects. A second lipid mobilizing peptide, sometimes called compound II (CII) or AKHII has been found in the glandular lobes of ***Schistocerca*** (Carlsen, Herman, Christensen and Josefsson 1979) and ***Locusta*** (Gäde 1981) CC. CII is a blocked octapeptide that seems to have an action on flight fuel metabolism similar to AKH.

Exogenous dibutyryl cyclic AMP mimics AKH action in vivo (Gäde and Holwerda 1976) and in vitro (Spencer and Candy 1976); levels of cyclic AMP increase in fat body after AKH injection (Spencer and Candy 1976, Gäde and Beenakkers 1977) and during flight, and this effect appears to be calcium dependent (Spencer and Candy 1976). However, direct demonstration of an effect of AKH in activating triacylglycerol lipase has not been done.

In a resting locust the primary lipid transport protein is complexed with a carotenoid and has been called A yellow. During flight or starvation, a new lipoprotein complex, A+, appears in the hemolymph. Injection of AKH results, after a delay of 10−15 min, in the formation of A+ from diacylglycerol from the fat body and non-lipid-carrying proteins already present in the hemolymph (Mwangi and Goldsworthy 1976, 1977). Mwangi and Goldsworthy (1977) suggest that the action of AKH in A+ formation is indirect via lipid loading of A yellow. However, Van der Horst, Van Doorn and Beenakkers (1979) prefer the view that AKH plays a primary role in causing the hemolymph proteins to associate to form A+. This question has not been resolved.

AKH can apparently directly affect the flight muscles, favoring lipid metabolism over that of carbohydrate. The exact mechanism and site of action for AKH on flight muscle is not known. In ***Locusta***, injections of CC extract even in high doses do not have any effect on levels of either cAMP (Gäde and Holwerda 1976) or cGMP (Worm 1980) in flight muscles. Nor do these nucleotides increase during flight. However, uptake of diacylglycerol by working flight muscle can be stimulated by CC extracts. Robinson and Goldsworthy (1977) suggest that hormone extracts stimulate entry of diacylglycerols indirectly by increasing the flux of fatty acids into mitochondria.

AKH also appears to inhibit protein synthesis in vivo and in vitro (Carlisle and Loughton 1979). This effect is not restricted to specific proteins such as vitellogenins but rather is a general effect.

The Effect of JH and AKH on Migratory Behavior of *Danaus plexippus*

Populations of monarch butterflies in North America undergo dramatic migrations to overwintering areas each fall. These butterflies travel from Canada and northern United States to overwintering sites in southern California, Florida and Mexico and migrate back again to the north the following spring. In the fall, decreasing day lengths and lower temperatures appear to affect the neuroendocrine system in such a way that the activity of the CA and possibly the brain neurosecretory cells is altered (Herman 1973, Barker and Herman 1976, Herman this volume). It is clear that monarchs of the fall generation are physiologically and behaviorally different from those of the summer generations. Herman (1973, this volume) has shown that winter animals from the California populations are reproductively inactive owing at least in part to inactive CA. Juvenile hormone titer determinations done on field-collected animals (Lessman and Herman 1983) indicate a decrease in JH titers associated with the southward flight of the monarch and an increase associated with northward journeys. If lower titers of JH stimulate migratory flight while higher titers or longer exposure to the hormone are necessary for ovarian development, it is possible that changing titers of JH during the migratory and reproductive periods govern which activity will predominate as is the case with *Oncopeltus fasciatus*.

Dallmann and Herman (1978) found evidence of an adipokinetic hormone in monarch CC extracts which appears to elevate hemolymph diacylglycerols during flight and may act in much the same way the locust AKH does. Rankin, McAnelly and Bodenhamer examined flight behavior in *D. plexippus* to determine (1) whether an oogenesis flight syndrome exists in this species, (2) the effect of retrocerebral gland removal and JH replacement therapy on flight, and (3) the effect of AKH and JH on flight behavior of intact animals.

In the first experiment, animals were lab-reared under 16L:8D photoperiod as caterpillars and switched to 12°C, 11.5:12.5 L:D as adults; in a second experiment animals were field collected as spring migrants. Flight activity decreased with ovarian development in both groups. The decrease was much more striking in lab-reared animals (Fig 7A) than in spring migrants (Fig 7B)(Rankin et al., in press). Possibly spring migrants, which are emerging from the winter diapause, tolerate more ovarian development as an adaptation for rapid exploitation of the northern breeding grounds.

In contrast, in males, greater reproductive development is correlated with increased flight activity (Fig 7C). Since reproductive tract development in males is stimulated by JH, this correlation, along with the results outlined below, may indicate that longer exposure or higher titers of JH result in both enhanced flight activity and development of the reproductive tract.

The influence of juvenile hormone (JH) and adipokinetic hormone (AKH) treatment on flight of intact animals was examined using animals that were either field-collected during their migration or collected from diapause aggregation sites in Mexico. In the first experiment, animals were collected as migrants in late October, 1982, held at 10−12°C, 11.5:12.5 L:D for about 1 month. All butterflies were flight tested once before treatment to determine flight proclivity and then divided into 4

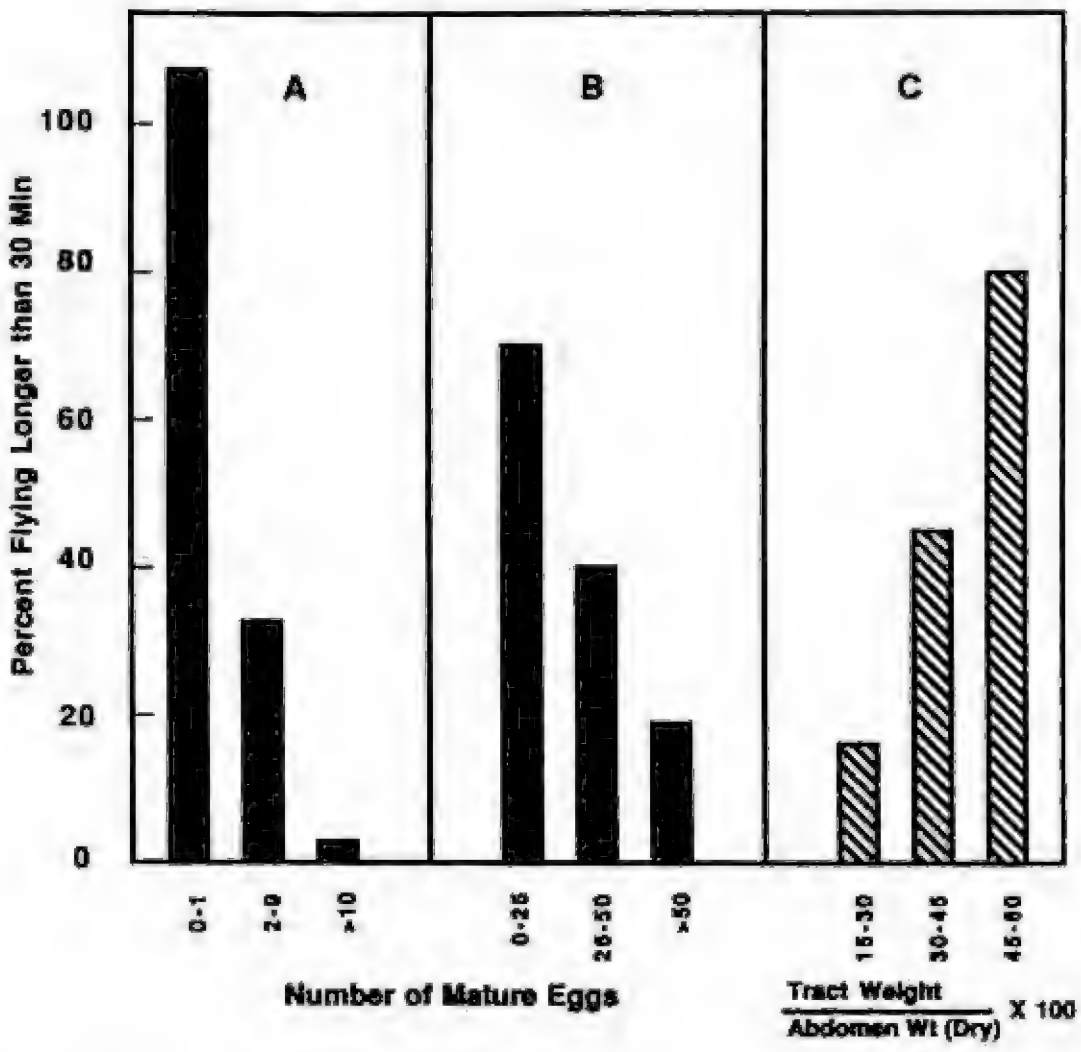

Figure 7

Oogenesis flight syndrome in monarch butterflies a. Percent of a lab-reared population making a continuous flight longer than 20 min with respect to ovarian development as measured by number of mature (chorionated) eggs in the reproductive tract.

b. Percent of a population of field-collected spring migrants making at least one continuous flight during a single flight test, with respect to ovarian development as measured by number of chorionated eggs in the reproductive tract.

c. Percent of field-collected and lab-reared males making 20 min flights, with respect to testis development. (From Rankin et al., in press.)

groups, each of which received an equal number of fliers and non-fliers as determined by the initial flight test. Five to seven days after the initial flight test, animals received hormone or carrier injections and were flight tested. A second treatment and flight test were given two days later.

Animals in a second experiment were collected in late January from Mexican aggregation sites, returned to Austin by airplane and maintained for two weeks as above. The treatment-flight test protocol was the same as in Experiment 1, as were the results; data for the two experiments were pooled and are shown in Figure 8.

AKH alone had a significant stimulatory effect on flight in both post-treatment flight tests while JH injections caused a significant increase in flight behavior but only in the second flight test of each experiment (Fig 8). It seems that the effect of AKH on flight behavior is immediate, while the JH effect requires some time (at least more than 2 hours) to develop. Both hormone treatments stimulate flight activity to an apparently equal degree and their effects were not additive (Rankin et al. in press).

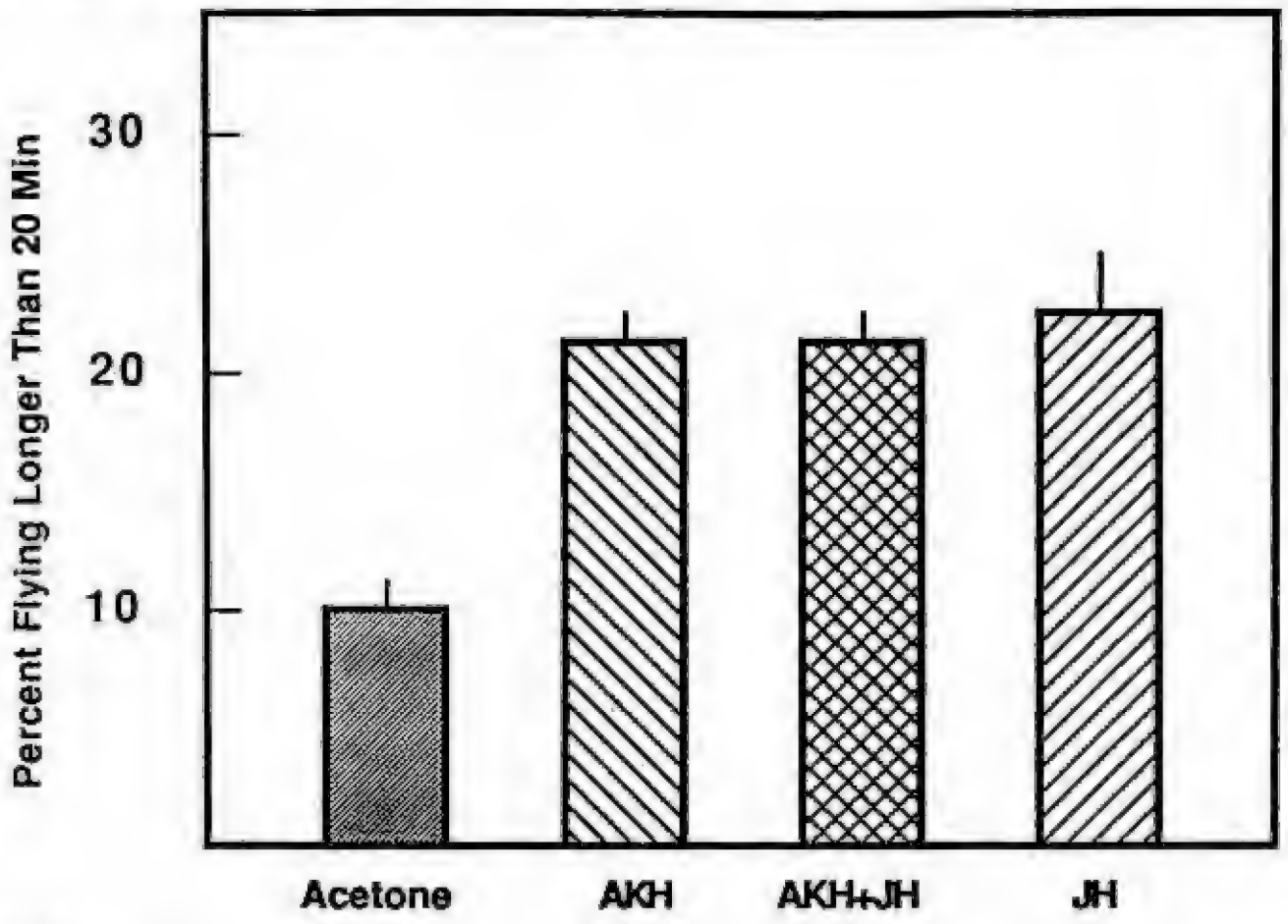

Figure 8

Effect of AKH and JH on flight behavior of intact *Danaus plexippus* tested on a stationary swivel tether (from Rankin et al., in press) (n = 50, acetone; 54, AKH; 55, AKH+JH; 54, JH).

In order to investigate the effect of JH on flight behavior, monarchs were allatectomized and given JH replacement therapy, and flight behavior was monitored. Animals were maintained at 10−12°C in short day photoperiods and were flight tested 7 days after surgery and every three days thereafter. Hormone or carrier treatments began on day 19 and continued at 3 day intervals until the termination of the experiment. The CC-CA-X group was divided into three groups on day 19, one of which received 20 μg JH I in hexane, the second 0.5 μl of hexane, and the third remained untreated.

Allatectomy was seen to significantly decrease and JH replacement therapy to restore flight activity in these populations (Fig 9). Animals were dissected at the termination of the experiment and examined for amount of reproductive tract development and for possible regeneration of the retrocerebral complex. No evidence of regeneration was observed. Number of mature eggs in sham-operated animals ranged from 0−118 with a mean of 23.6, and ranged in unoperated controls from 0−75 with a mean of 34.6. None of the allatectomized, untreated animals had mature oocytes, while 2 of the 6 hexane-treated females did, with a mean of 3.5 eggs. Allatectomized, JH-treated animals had from 3−59 mature eggs with a mean of 21.3. Why hexane treatment stimulated oogenesis (and flight) to a slight degree is not clear. Many precautions were taken against solvent contamination, but the data suggest that we may have had some JH contamination of the hexane. Alternatively, hexane may act as a weak JH mimic in this species (Rankin et al. (in press).

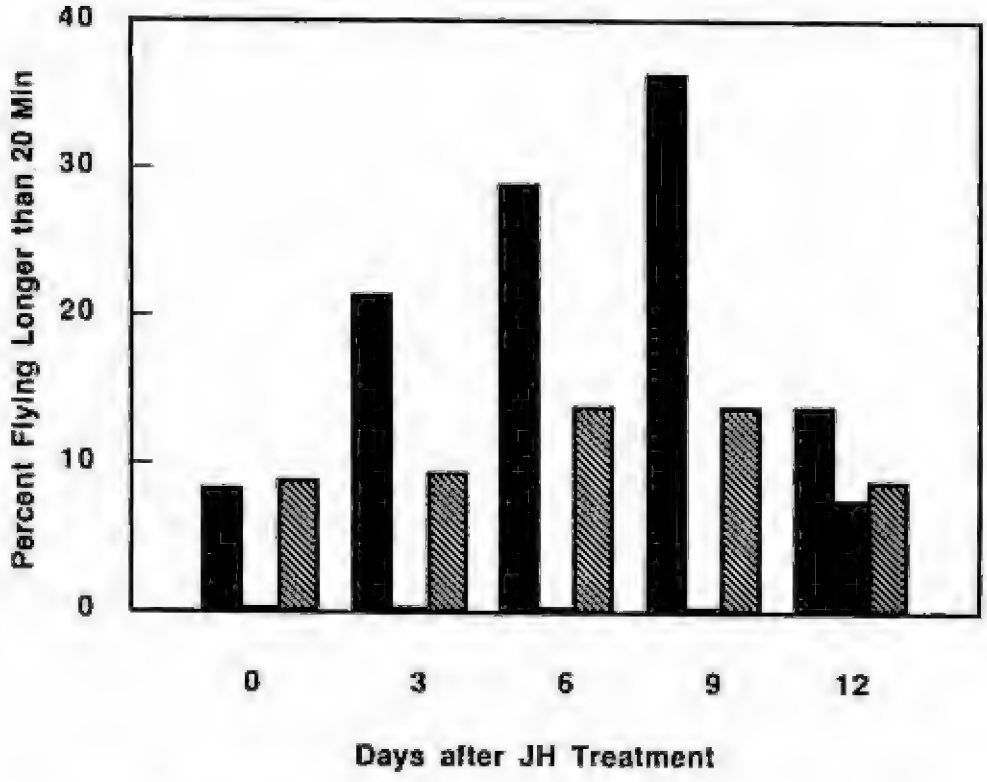

Figure 9

Effect of Allatectomy and JH replacement therapy on flight in *Danaus plexippus*. JH was applied in 0.5 μl of acetone or hexane to CC-CA-ectomized animals on day 19 and every three days thereafter prior to flight-testing. Animals were flight tested for 1 hour at three day or 1 week intervals in front of a low speed fan, with or without a spotlight for added heat. During the 1 hour test, animals were monitored at 2 minute intervals; notation was made as to whether the animal was flapping its wings, quivering the wings, or stopped. Minutes of continuous flight and % flying longer than 20 min were noted. (n = 14, CA-CCX + hexane or nothing, black bars; n = 21, sham-operated; n = 23 unoperated controls—graphed together as diagonally striped bar; n = 15 CA-CCX + JH, shaded bar) (from Rankin et al. in press).

These experiments suggest that the monarch butterfly, like *Oncopeltus fasciatus*, increases flight activity in direct response to JH. We should add, however, that because of difficulties in identifying migratory as opposed to trivial flight in a tethered flight assay with these butterflies, these results must be considered preliminary. Further, because of the length of time animals were held in the cold, all experiments were done on the equivalent of diapausing winter or early spring animals, i.e., all had experienced short day length as young adults and a prolonged period at 10−12°C before flight testing. The question of JH stimulation of the southward flight when JH titers are low or decreasing and the ovaries are undeveloped has not been addressed by these experiments. Other factors such as AKH may be involved in flight stimulation, at least in the fall, and JH may simply add to that effect during the spring migration.

OCTOPAMINE

The biogenic amine, octopamine, is the substance most recently implicated in the neuroendocrine control of flight behavior. It seems to play a pivotal role in at least some species in stimulating the neuromuscular flight motor. It also seems to be involved in flight fuel metabolism directly and possibly indirectly as well through stimulating release of AKH.

In *Schistocerca*, octopamine titers rise dramatically during the first 10 min of flight and then decline rapidly (Goosey and Candy 1980). Sites of release may be nerves emanating from the thoracic ganglia (Goosey and Candy 1982). Octopamine may affect both flight muscles and fat body. In *Locusta* fat body in vitro, octopamine stimulates production of cAMP which suggests that the biogenic amine may facilitate rapid mobilization of diacylglycerol or other fuel during the first minutes of flight. Octopamine also stimulates the oxidation of glucose and diacylglycerol in working flight muscle, though its effect on glucose is more pronounced (Candy 1978). Octopamine may be involved in early metabolism of carbohydrate and the switch from carbohydrate to lipid in later stages of flight.

Octopamine has also been shown to elicit flight ***behavior*** in vivo and activity of the flight motor in vitro. Injections of octopamine or its agonist chlordimeform, into the hemolymph of adult ***Manduca sexta*** elicited bouts of wing flapping in a dose-related fashion and increased the sensitivity of moths to mechanical stimulation (Kinnamon, Klaassen, Kammer and Claassen 1985). Comparable results were obtained when pharate adults were similarly injected. Treatment with chlordimeform or octopamine on day 15 of the 19 day pupal period resulted in almost continuous production of the flight motor pattern until a few hours before eclosion. The response was dose and age dependent (Kinnamon et al 1985).

When these compounds were superfused over or injected directly into the mesothoracic ganglion, similar enhancement of flight motor activity and increased sensitivity to mechanical stimuli were observed.

Octopamine also appears to enhance neuromuscular transmission and the rate of contraction in developing *M. sexta* flight muscle (Klaassen and Kammer 1985).

In contrast to the observations of Kinnamon et al. (1985), injection of octopamine or other related compounds into other insects has generally shown no effect on flight ***behavior***. For example, injection of various doses of octopamine into *Oncopeltus fasciatus* did not affect flight behavior either immediately or after 2 days (Rankin, unpublished results). Similarly, injection of octopamine into the hemolymph of locusts did not elicit flight or any other behavior (Sombati and Hoyle 1985). However, when physiological doses of octopamine were iontophoresed into specific regions of the metathoracic ganglion, bouts of rhythmic stepping behavior or flight behavior were elicited, depending on the location of the electrode. The flight motor output was always bilateral and proportional to the amount of amine delivered to the preparation. Interestingly, octopamine iontophoresed into the terminal abdominal ganglion ***inhibited*** digging or oviposition motor patterns from that ganglion (Sombati and Hoyle 1985).

DISCUSSION

In at least three species of highly migratory insects, JH has been shown to stimulate both flight and oogenesis. This apparently dual action of the hormone is by no means universal; as noted above, in some insects, JH can cause flight muscle histolysis or have no obvious effect on flight behavior (Rankin, unpublished). If JH evolved originally as a hormone controlling metamorphosis, its effect on reproductive development in the adult probably evolved secondarily. Tertiary effects of the hormone such as control of caste determination, aggressive behavior or flight behavior seem to have evolved separately in many insect groups. JH control of migratory behavior may have developed as a response to selection associated with a colonizing life style in which, ideally, both flight and reproductive parameters would be maximized. The stimulation of both flight and oogenesis by the same hormone would be an efficient mechanism for production of a migrant in which at least early reproductive output would be maximized in the newly colonized habitat. The argument gets more complex, however, when a period of diapause, involving low JH and cessation of oogenesis is involved. In this case one must propose that either (1) a second factor is necessary for oogenesis, and in its absence JH only stimulates flight (this may well be the situation for *H. convergens*) and/or (2) that higher titers of (or perhaps different periods of exposure to) the hormone are necessary to stimulate reproduction than are necessary to induce migratory flight. This may be the case for *Oncopeltus fasciatus* in, for example, its response to starvation. (3) A third possibility is that migratory behavior can be stimulated by another hormone, such as AKH, as well as by JH, as may perhaps be true for the monarch butterfly in its southward flight. However, more precise information regarding effects of endocrine manipulation on clearly identified migratory behavior in the monarch is necessary before the actual role of JH in long distance movement in this species can be precisely determined.

Octopamine may be a key element in the neuroendocrine control of flight behavior and metabolism, at least in locusts. It appears to simultaneously act as (1) a neurotransmitter or neural modulator stimulating the flight motor, (2) as a neurohormone eliciting flight fuel release and metabolism and (3) perhaps as a neurotransmitter stimulating AKH release. A fruitful area for future research in this area would seem to be to investigate the interaction of octopamine and JH in controlling flight behavior and reproduction in those species in which JH seems to play a role in both.

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